A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE) PART IV

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INTRODUCTION

In previous parts of this series I have revised species-groups possessing common or related structural peculiarities and, in most cases, similar feeding habits. The present paper deals with a greater variety of structural and trophic types and many of the species show no obvious relationship to one another. With one exception, the species described below fall into three groups, namely, structurally generalized insectivorous species, specialized mollusc-eaters and species showing various degrees of structural and adaptational intermediacy between the other two groups. The exceptional fish, *Haplochromis martini* is a piscivorous predator; it is included simply because of its overall resemblance to one of the insectivorous species described here.

Formerly, some of the generalized species reviewed in this paper were synonymized with one of the mollusc-eaters (*H. ishmaeli*); the others are included because of various resemblances to species now resurrected and redefined. One such is *Haplochromis cinereus*, a species previously considered to be the extant representative of the ancestral type from which at least part of the present flock had evolved. These

views on the central evolutionary position of *H. cinereus* are no longer tenable since the " species " thought to be *H. cinereus* was a complex of several distinct species, some more generalized than the others. *Haplochromis cinereus, sensu stricto* is, in fact, an anatomically somewhat specialized derivative from an even more generalized form.

The most outstanding structural character in many of the species described below is an increase in the strength and size of the pharyngeal bones and musculature. As might be expected, these changes are reflected in the diet of the species, which usually include Mollusca as an important element in their food. Two species, *H. ishmaeli* and *H. pharyngomylus*, feed almost entirely on snails and bivalves.

Those species with the pharyngeal mill in an intermediate stage of hypertrophy are able to deal with small molluscs and also with the tubicolous larvae of certain Trichoptera, an otherwise infrequent element in the food of insectivorous *Haplochromis* without strengthened pharyngeals.

By crushing their molluscan prey within the pharynx these species stand in sharp contradistinction to the other groups of mollusc-eating *Haplochromis* in Lake Victoria. Species in this latter group remove the snail from its shell by holding the foot between the jaws and then levering the soft parts free before ingestion takes place (Greenwood, 1956*a* and 1957).

Haplochromis lacrimosus (Blgr.) 1906

(Text-fig. 1)

Tilapia lacrimosa (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7) **17**, 450 ; *Idem*, 1907, *Fish. Nile*, 515 ; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 234, fig. 154.
Haplochromis cinereus (part) Regan, 1922, *Proc. zool. Soc. London*, 166.

Lectotype. An adult male 76 mm. standard length (B.M. [N.H.] 1906.5.30.471) from Entebbe.

Description, based on 36 specimens (including the lectotype and 10 paratypes) 66·0–97·0 mm. S.L.

Depth of body 31·8–38·7 (M = 35·5) per cent of standard length, length of head 30·8–35·5 (M = 33·5) per cent. Dorsal head profile straight or slightly curved, sloping moderately steeply. Preorbital depth 13·6–18·0 (M = 15·5) per cent of head length, showing weak positive allometry with standard length ; least interorbital width 20·8–26·9 (M = 23·5), snout length 26·6–32·2 (M = 29·6) per cent. Diameter of eye 26·1–32·6 (M = 30·4) per cent of head, ratio of eye diameter to preorbital depth 1·5–2·3 (mode 2·0) ; depth of cheek 17·6–23·5 (M = 20·8) per cent. Caudal peduncle 15·0–19·2 (M = 17·2) per cent of standard length, 1·2–1·8 (mode 1·5) times as long as deep.

Mouth horizontal or almost so ; jaws equal anteriorly, the lower 31·4–41·3 (M = 37·1) per cent of head and 1·2–2·0 (mode 1·6) times as long as broad. Posterior tip of the maxilla extending to the vertical to the anterior orbital margin or slightly beyond, rarely not quite reaching the anterior orbital margin.

Gill rakers variable, from moderately stout to slender ; 7–9 (mode 8), rarely 6 on the lower part of the first gill arch, the lowermost two or three reduced.

Scales ctenoid ; lateral line with 31 (f.5), 32 (f.21) or 33 (f.8) scales ; cheek with 2 or 3 (rarely 4) series ; 6 or 7 (rarely $5\frac{1}{2}$) between the lateral line and the dorsal fin origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases. Scales of the pectoral region small or moderate.

Fins. Dorsal with 24 (f.19) or 25 (f.16) rays, anal with 11 (f.19), 12 (f.16) or 13 (f.1), comprising XV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 82·5–100·0 (M = 88·5) per cent of head. Caudal truncate or subtruncate.

Teeth. The outer row in both jaws is composed of unequally bicuspid, relatively slender and sometimes slightly recurved teeth. Rarely, a few unicuspid teeth may occur anteriorly in this row ; likewise a few posterolateral teeth in the upper jaw

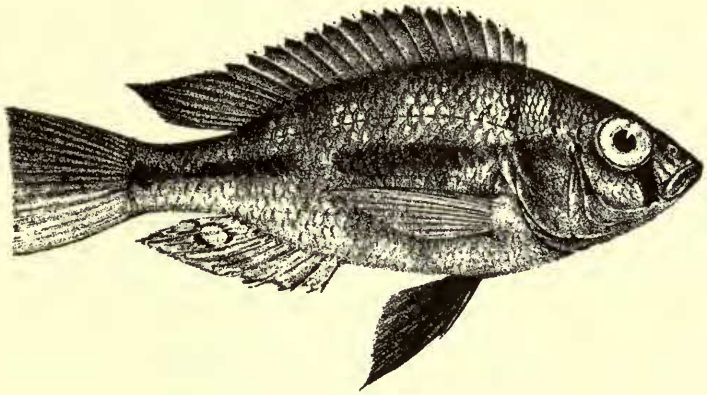

FIG. 1. *Haplochromis lacrimosus ;* lectotype (from Boulenger, *Fishes of the Nile*).

may be unicuspid. There are 40–60 (mode 54, modal range 48–54) teeth in the upper jaw.

Teeth in the inner series are tricuspid and implanted at a slight, posteriorly directed angle (cf. *H. cinereus* where the inner teeth lie almost horizontally) ; there are 2 or 3 (rarely 4) rows of inner teeth in the upper jaw and 2 (less commonly 3, rarely 4) in the lower.

Lower pharyngeal bone triangular and slender ; a few slightly enlarged but bicuspid teeth may occur in the median tooth-rows.

Coloration. The colours of live fishes are unknown.

Preserved material : Sexually active males. Ground colour yellowish-silver, chest dusky ; a dark lachrymal stripe is always present and in some specimens it may extend obliquely upwards through the eye and on to the nape ; there are usually two transverse bands across the snout.

Two common patterns of body markings are known. (i) A large mid-lateral blotch

situated slightly posterior to the pelvic fin insertion and a mid-lateral stripe running from a point above the second anal ray on to the caudal fin.; a faint transverse bar is visible immediately posterior to the edge of the operculum and two others lie between the mid-lateral blotch and the origin of the posterior stripe. The blotch itself appears to be the intensified mid-portion of a vertical bar.

(ii) Nine, close-set and ventrally ill-defined transverse bars on the flanks ; ventrally, the bars tend to run into one another so that the lower region of the flank is steely-grey.

All fins, except the pelvics, hyaline, the upper part of the caudal sometimes weakly maculate, the mid-part dark ; anal with two or three ocelli ; pelvic fins black.

Females and quiescent males. Ground colour greyish-silver, brownish above. Seven to nine faint transverse bars on the flanks, not reaching the ventral or dorsal outlines of the body. All fins hyaline.

Distribution. At present, *H. lacrimosus* is known with certainty from Lake Victoria ; Pappenheim & Boulenger (1914) recorded a specimen from Lake Edward, but I have not been able to examine their material.

Ecology : Habitat. No precise details are available for fishes already in the collections of the B.M. (Nat. Hist.) ; specimens collected by E.A.F.R.O. come from only two localities, both exposed, sandy beaches with the water depth less than 20 feet. Thus, it is impossible to generalize on the habitat preferences of *H. lacrimosus*.

Food. The stomach and intestinal contents of twenty fishes were examined ; with one exception (a fish from Entebbe) these specimens were caught at one time and at a single locality (Majita, Tanganyika Territory). The gut contents of the sixteen specimens containing food were varied. Twelve fishes contained fine sand-grains, bottom detritus (including fragments of plant epidermis and diatom frustules) and some Cladocera ; five contained remains of insect larvae (probably Diptera), one an adult dipteran, one the remains of a larval *Povilla adusta* Navás (Ephemeroptera) and one an insect egg-mass. Two fishes yielded, besides insect fragments, the remains of an oligochaet worm, whilst two others each contained the foot and soft parts of a snail. From these scanty and topographically restricted data, *H. lacrimosus* should perhaps be classified as a bottom-feeding omnivore.

Breeding. The breeding habits are unknown. Two of the smallest fishes (male and female, both 66·0 mm. S.L.) are adult. It seems possible that adult males reach a larger maximum size than do females.

Affinities. Haplochromis lacrimosus is one of the structurally and ecologically generalized species of Lake Victoria. Its most striking and apparently diagnostic character is the markings of male fishes ; but, it must be stressed that coloration is known only from preserved material. In general appearance *H. lacrimosus* resembles *H. pallidus* (see p. 233) but the two species differ in several characters besides male coloration.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.471 (Lectotype *Tilapia lacrimosa*)	Entebbe	Degen
B.M. (N.H.).—1906.5.30.472–478	,,	,,
,, 1906.5.30.483–484	Bunjako	,,
,, 1906.5.30.488–489	Buganga	,,
,, 1907.5.7.81–82	Buddu Coast	Simon
,, 1908.10.19.2–5	Sesse Islands	Bayon
,, 1959.4.28.24	Entebbe Harbour	E.A.F.R.O.
	Tanganyika	
,, 1959.4.28.1–23	Majita	,,

Haplochromis pallidus (Blgr.) 1911
(Text-figs. 2 and 3)

Tilapia pallida (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 74; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 231–2.
Labrochromis pallidus Regan, 1920, *Ann. Mag. nat. Hist.* (9), **5**, 45 (footnote).
Haplochromis cinereus (part), Regan, 1922, *Proc. zool. Soc. London*, 166.

This synonymy is tentative, as I have been unable to locate three specimens of *T. pallida* which Regan (1922) referred to *Haplochromis guiarti* (Pellegrin). Regan's genus *Labrochromis*, based on a skeleton wrongly identified as *T. pallida*, is discussed on page 275.

Description, based on twenty specimens (including the holotype and four paratypes) 43–74 mm. S.L.

Depth of body 33·3–38·8 (M = 35·4) per cent of standard length, length of head 32·3–35·3 (M = 34·1) per cent. Dorsal head profile straight or slightly curved, sloping at about 30°–40°. Preorbital depth 13·2–18·2 (M = 16·5) per cent of head; least interorbital width 21·0–30·0 (M = 24·7) per cent. Snout as long as broad or slightly longer; its length 29·1–33·4 (M = 31·2) per cent of head; diameter of eye 26·1–33·4 (M = 29·5) per cent, ratio of eye diameter to preorbital depth 1·5–2·3 (mode 1·7); depth of cheek 19·0–25·0 (M = 21·7) per cent of head. Caudal peduncle 14·2–18·5 (M = 16·2) per cent of standard length, 1·2–1·7 (mode 1·2) times as long as deep.

Mouth horizontal; jaws equal anteriorly, the lower 32·2–40·9 (M = 37·6) per cent of head and 1·4–1·8 (mode 1·6) times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or slightly beyond.

Gill rakers short and stout (slender in one specimen), 7–9 (mode 9), rarely 10, on the lower part of the first arch, the lowermost 1–4 (or even 5) rakers greatly reduced.

Scales ctenoid; lateral line with 31 (f.6), 32 (f.13) or 33 (f.1) scales; cheek with 2 or 3 (rarely 4) series; 6 or 7 (occasionally 5) between the lateral line and the dorsal fin origin, 6 or 7 (occasionally 8) between the pectoral and pelvic fin bases. Scales on the chest rather small.

Fins. Dorsal with 24 (f.5) or 25 (f.15) rays, anal with 11 (f.3) or 12 (f.17), comprising XV–XVI, 8–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Caudal truncate ; pectoral fin 78·0–87·0 (M = 81·0) per cent of head.

Teeth. The outer row in both jaws is composed of unequally bicuspid, moderately stout teeth implanted erectly. In most fishes more than 67 mm. S.L. some unicuspid teeth occur postero-laterally in the upper jaw. The holotype (the largest specimen examined) has only weakly bicuspid teeth in the outer row. Three small specimens from near the Ripon Falls have somewhat more slender outer teeth than other specimens. There are 36–48 teeth in the upper outer series ; no clear-cut mode can be determined from the sample studied.

The small and tricuspid inner teeth are implanted at a very slight angle and arranged in 3 (rarely 2) rows in the upper jaw and 2 or 3 rows in the lower.

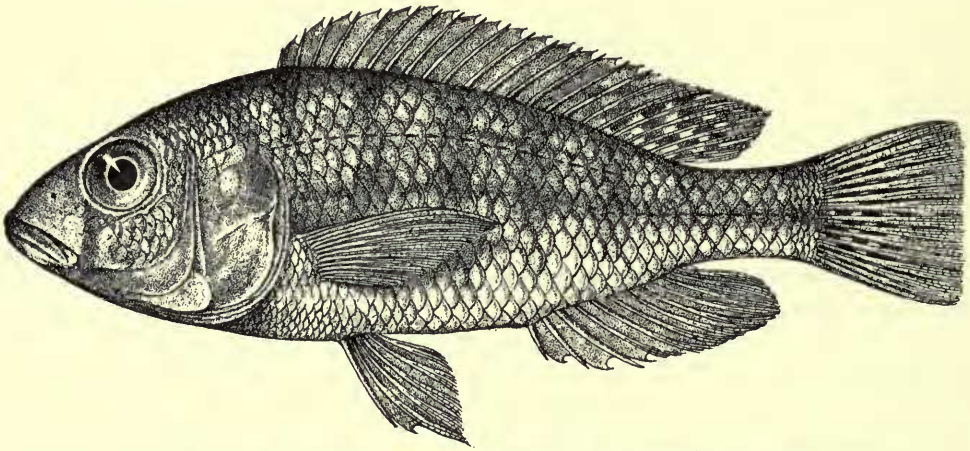

FIG. 2. *Haplochromis pallidus ;* holotype (from Boulenger, *Ann. Mus. Genova*).

Lower pharyngeal bone triangular, usually slender but slightly thickened in three specimens. Most fishes have the two median rows of teeth slightly enlarged (especially the most posterior one or two pairs) ; in a few, all the pharyngeal teeth are slender.

Coloration. The colours of live fishes are unknown.

Preserved material. Adult males. Ground colour greyish, with faint traces of up to seven dark transverse bars on the flank and caudal peduncle ; branchiostegal membrane greyish. A distinct, vertical lachrymal stripe, continued at an angle, runs through the centre of the eye ; a very faint stripe runs from the posterior orbital margin to the angle of the preoperculum. Dorsal fin greyish, with dark lappets and a dark band along the basal two-thirds of the fin anteriorly, narrowing to the basal third or quarter posteriorly. Caudal dark proximally and along the mid-line. Anal hyaline, with two large, dead-white ocelli. Pelvics black, darkest laterally.

Females and immature males. Ground colour greyish-silver, six or seven faint transverse bars on the flanks and, in some, two bars on the caudal peduncle ; a very faint lachrymal stripe. All fins hyaline.

Boulenger's (1911) account of preserved coloration differs somewhat from that given above, but as his material represented at least two and possibly three species, the discrepancies are not considered significant.

Distribution. Known only from Lake Victoria, unless the locality " Jinja, Ripon Falls " for specimens nos. 1911.3.3.127–130 implies that these fishes were caught *below* the falls in the Victoria Nile.

Ecology. Habitat. The only precise bionomic data available are for those specimens collected by E.A.F.R.O. All these were from one locality, an exposed, shallow and sandy beach near Entebbe Airport.

Food. Thirteen of the sixteen fishes examined had ingested matter in the stomach and intestine ; all these specimens were collected at one locality and at the same

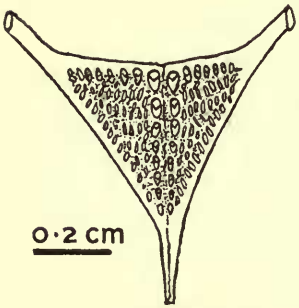

FIG. 3. *Haplochromis pallidus;* lower pharyngeal bone, occlusal view.

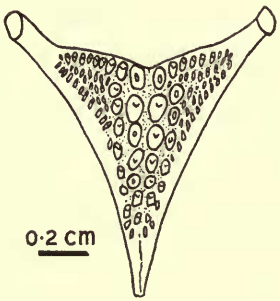

FIG. 4. *Haplochromis riponianus ;* lower pharyngeal bone, occlusal view.

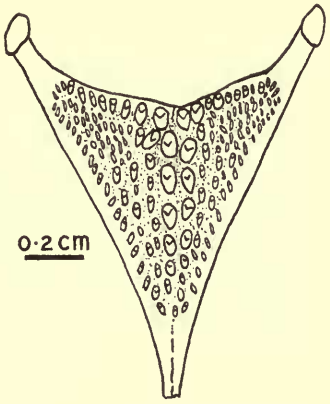

FIG. 5. *Haplochromis saxicola ;* lower pharyngeal bone, occlusal view.

time. Except for three fishes, all contained moderately large quantities of bottom debris (sand grains, diatom frustules and fragments of plant tissue) together with fragmentary insect larvae (? Diptera). The exceptional specimens contained only bottom detritus.

Breeding. Haplochromis pallidus is a female mouth brooder ; the two smallest fishes examined (a male 54 mm. S.L. and a female 58 mm. S.L.) are both adult.

Affinities. Haplochromis pallidus must be considered one of the many small and generalized species in Lake Victoria. Within this group it is extremely difficult to suggest phyletic relationships because the degree of inter-specific differentiation is so slight. In general appearance *H. pallidus* perhaps comes nearest to *H. lacrimosus,* from which species it is distinguished by a higher modal number of gill rakers (9 cf. 8), fewer and somewhat stouter teeth, a lower modal eye/preorbital ratio (1·7 cf. 2·0) and particularly, by differences in the preserved coloration of male

fishes. The nature of both oral and pharyngeal dentition suggests that a "*pallidus*"-like species could have been ancestral to the adaptational grade at present represented by *Haplochromis humilior* (see p. 252).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12912)	Jinja	Bayon
B.M. (N.H.).—1911.3.3.127–130	Jinja, Ripon Falls	,,
,, 1959.4.28.25–40	Entebbe, Airport beach	E.A.F.R.O.

Haplochromis macrops (Blgr.) 1911

(Text-fig. 6)

Haplochromis stanleyi (part) Boulenger, 1914, *Cat. Afr. Fish.* **3**, 295.
Haplochromis ishmaeli (part) Boulenger, 1914, *tom. cit.* 293.
Tilapia macrops Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 73. pl. III, fig. 1; *Idem*, 1914, *Cat. Afr. Fish.* **3**, 238.
Haplochromis macrops (part, i.e. the species as described but excluding the tentative synonymy of *Astatotilapia jeanneli* Pellegrin), Regan, 1922, *Proc. zool. Soc. London*, 166.

Description, based on forty specimens from Lake Victoria (including the holotype [Genoa Museum] and one of the paratypes) 66–91 mm. S.L.

Depth of body 32·5–38·2 (M = 35·8) per cent of standard length, length of head 31·0–35·1 (M = 33·0) per cent. Dorsal head profile straight or slightly curved, sloping at a moderate angle (*ca.* 35°–40°). Preorbital depth 11·5–16·3 (M = 14·2) per cent of head, least width of interorbital 26·6–32·2 (M = 29·7) per cent. Snout as broad as long or slightly broader, its length 26·6–31·0 (M = 29·0) per cent of head, diameter of eye 28·6–35·4 (M = 33·0) per cent, ratio of eye diameter to preorbital depth 2·0–2·9 (mode 2·3); depth of cheek 17·8–24·2 (M = 21·1) per cent of head. Caudal peduncle 14·1–18·4 (M = 16·8) per cent of standard length, 1·2–1·6 (mode 1·4) times as long as deep.

Mouth slightly oblique, posterior tip of the maxilla extending to the vertical to the anterior orbital margin or even as far as the pupil. Lower jaw 38·0–42·5 (M = 39·5) per cent of head, 1·4–2·2 (modal range 1·7–1·8) times as long as broad.

Gill rakers slender or, occasionally, relatively stout; 8–11 (mode 9) on the lower part of the first arch, the lower 1–4 rakers reduced.

Scales ctenoid; lateral line with 30 (f.6), 31 (f.17), 32 (f.13) or 33 (f.3) scales; cheek with 2 or 3 series. Five or 6 (occasionally 7) scales between the lateral line and the dorsal fin origin; 6 or 7 (occasionally 5, rarely 8) between the pectoral and pelvic fin bases. Scales on the pectoral region (relative to those on the ventral abdominal region) moderate to large.

Fins. Dorsal with 24 (f.6), 25 (f.30) or 26 (f.4) rays, anal with 11 (f.9), 12 (f.30) or 13 (f.1), comprising XV–XVII, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 68·0–96·0 (M = 84·0) per cent of head. Caudal truncate.

Teeth. The outer row of teeth in both jaws (except those situated postero-laterally in the upper) is composed mainly of bicuspid, moderately stout teeth. In certain fishes over 80 mm. S.L. some weakly cuspidate teeth may occur. *H. macrops* is, however, unusual in that the postero-lateral teeth in the upper jaw are generally tricuspid in fishes less than 85 mm. S.L. ; in larger individuals these teeth may be unicuspid. One aberrant individual has only tricuspid teeth in the upper, outer row ; the corresponding row in the lower jaw has a mixture of bi- and tricuspids, with the former predominating. There are 46–66 (mode 60, modal range 56–60) teeth in the upper, outer row.

The inner tooth-rows are made up of tri- and unicuspid teeth arranged in 2 or 3 (rarely 4) rows in the upper jaw and 1 or 2 (less commonly 3) rows in the lower. Inner teeth are implanted so as to stand erect or with a very slight, posteriorly directed slope.

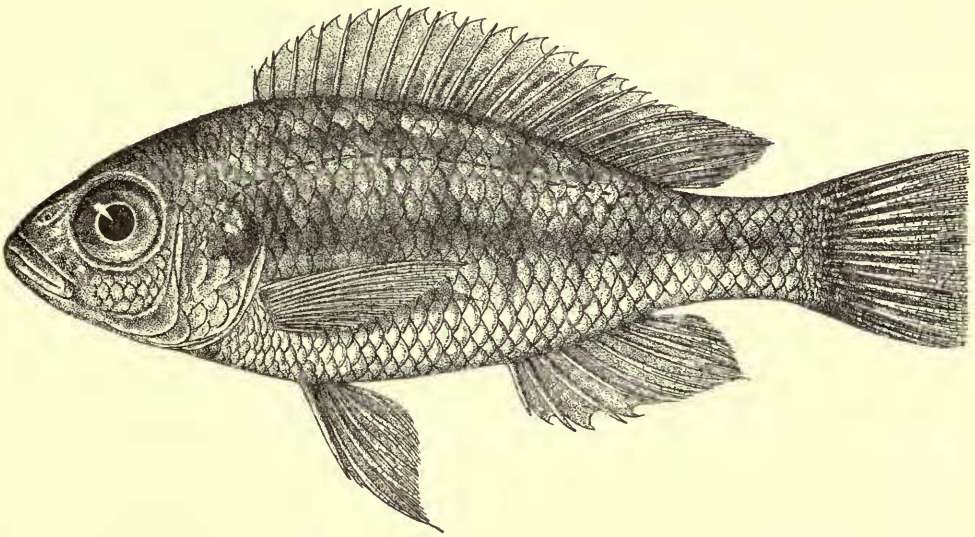

FIG. 6. *Haplochromis macrops ;* holotype (from Boulenger, *Ann. Mus. Genova*).

Lower pharyngeal bone triangular, not enlarged ; teeth fine and cuspidate.

Coloration in life. Sexually active males. Ground colour dusky to intensely black. Dorsal fin black, lappets and margin of the soft part red, as are the spots and blotches between the branched rays. Anal dusky with a diffuse red flush becoming more intense distally : ocelli yellow. Caudal dusky, ventral half with a red flush. Pelvic fins dusky yellow. *Quiescent males* have a female-type coloration, but with yellow anal ocelli and red spots on the soft dorsal. *Females.* Ground colour greyish-yellow to silver-grey. Dorsal and anal fins light yellow, caudal yellowish.

Colour of preserved material. Adult males. Dark blackish-brown, somewhat lighter, except in sexually active fishes, on the chest and branchiostegal membrane ; faint indications of six transverse bars on the flanks (generally not reaching the dorsal and ventral outlines) ; a dark but faint lachrymal stripe is visible in some specimens,

as is a faint dark bar along the preoperculum. Dorsal fin dark (especially along the basal third), lappets black. Caudal fin dark. Anal dark on the basal third to half, pale distally, with two or three ocelli. Pelvic fins black. *Females*. Brownish-yellow, some with eight or nine faint transverse bars on the flank and caudal peduncle. All fins hyaline but the caudal somewhat darker.

Distribution. Definite records of *Haplochromis macrops* are available only from Lake Victoria although there is an indication that the species may also occur in the Lake Edward basin. I have examined material identified as *H. macrops* from Lake Edward (one specimen B.M. (N.H.) Reg. No. 1933.2.23.397 ; see Trewavas, 1933) and from rivers flowing into Lake Edward (see Poll, 1939 and Poll & Damas, 1939). Of these latter specimens (twelve in all) only one (R. G. Mus. Congo 31095, det. David, 1936), from Rutshuru, compares closely with the Victoria population of *H. macrops*. I hesitate to identify the remaining Congo Museum specimens from Rutshuru (Reg. Nos. 64888–64899), but the single specimen from the B.M. (N.H.) seems most closely allied to *H. lividus* Greenwood of Lake Victoria. I have not been able to study the two specimens from Lake Edward (now in Berlin) which Pappenheim & Boulenger (1914) identified as *H. macrops*.

The single specimen (R. G. Mus. Congo 31095) from the Edward basin now referred to *H. macrops* differs slightly from the generality of Victoria fishes in having a somewhat larger eye and longer lower jaw ; it is an adult female, 73·0 mm. S.L. The principal morphometric characters of this fish are :

D*	H*	Po. %	Io. %	Eye %	Snt. %	Ck. %	Lj. %	C.P.*	Eye/Po.
32·8	31·4	15·2	30·4	37·0	30·4	21·7	43·4	15·0	2·4

* Per cent standard length.
% Per cent head length.

Dorsal XV, 9 ; anal III, 9 ; pectoral 91·3 per cent of head.

In characters of dentition and squamation this fish is similar to those from Lake Victoria.

Ecology. Habitat. The species is apparently confined to the shallow, sandy regions of the lake.

Food. The predominating food organisms in the stomachs and intestines of twenty-four fishes (mainly from one locality, but caught on different occasions) are sub-imaginal Ephemeroptera ; two fishes had, however, fed almost exclusively on winged termites (Isoptera) and colonial blue-green algae. Typical bottom debris and sand-grains usually found in the guts of other insectivorous *Haplochromis* were not recorded. The occurrence of sub-imaginal or adult insects and planktonic blue-green algae, together with the absence of bottom debris, suggests that *H. macrops* feeds at the surface or in mid-water. Since the algae were not digested and did not constitute a major proportion of the ingested matter, they may be taken accidentally as the fishes dart after insect prey.

Breeding. *Haplochromis macrops* is a female mouth-brooder. The smallest sexually active fish is a female 73 mm. S.L., the smallest adult male is 78 mm. S.L. It appears that males attain a larger maximum adult size than do females.

Affinities. As with most of the structurally and trophically generalized *Haplochromis* of Lake Victoria, the detailed affinities of *H. macrops* are impossible to determine. The similarities existing between *H. macrops* and *H. cinereus* are discussed elsewhere (p. 242). The two species differ in several characters, particularly in their dentition and the larger eye/preorbital ratio of *H. macrops* (2·0–2·9, mode 2·3, cf. 1·5–1·9, mode 1·8 for *H. cinereus*). Also, the gill rakers of *H. macrops* are finer and more numerous (mode 9) than in *H. cinereus* (mode 7).

The large eye and shallow preorbital of *H. macrops* serve to distinguish the species from most other members of the " generalized species " group.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12928) (Holotype)	Bussu	Bayon
B.M. (N.H.).—1911.3.3.137 (Paratype)	Bussu	Bayon
B.M. (N.H.).—1911.3.3.114–115	Jinja, Ripon Falls	,,
,, 1959.4.28.51–78	Beach near Nasu Point	E.A.F.R.O.
,, 1959.4.28.79–84	Buka Bay	,,
	Tanganyika	
,, 1959.4.28.85	Mwanza, Capri Bay	,,
,, 1959.4.28.86	Majita	,,
,, 1959.4.28.87	Beach near Majita	,,

Haplochromis cinereus (Blgr.) 1906
(Text-fig. 7)

Paratilapia cinerea Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 439 ; *Idem*, 1907, *Fish. Nile*, 478 ; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 344.
Haplochromis stanleyi (part), Boulenger, 1915, *tom. cit.*, 295.
Tilapia lacrimosa (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 450 ; *Idem*, 1915, *tom. cit.*, 234.
Haplochromis cinereus (part), Regan, 1922, *Proc. zool. Soc. London*, 166.
Haplochromis melanopus (part), Regan, 1922, *op. cit.* 165.

Description, based on twelve specimens (including the holotype) 71–81 mm. S.L. Depth of body 34·6–39·0 per cent of standard length, length of head 30·8–37·3 (M = 34·7) per cent. Dorsal head profile straight or slightly curved, sloping at *ca.* 40°–50°. Preorbital depth 15·0–18·0 (M = 16·4) per cent of head length, least interorbital width 23·3–28·0 (M = 25·3) per cent. Snout as long as broad or slightly longer, its length 29·2–34·6 (M = 32·2) per cent of head, eye diameter 26·2–32·0 (M = 28·7) per cent, ratio of eye diameter to preorbital depth 1·5–1·9 (mode 1·8). Depth of cheek 20·8–26·0 (M = 23·0) per cent of head. Caudal peduncle 15·7–18·7 per cent of standard length, 1·4–1·6 times as long as deep.

Mouth horizontal or very slightly oblique ; jaws equal anteriorly, the lower 34·6–41·3 (M = 37·7) per cent of head and 1·4–1·8 (mode 1·6) times as long as broad. Lips slightly thickened. Posterior tip of the maxilla extending almost to the vertical through the anterior orbital margin or as far as the eye.

Gill rakers moderately stout, 7–9 (mode 7) on the lower part of the first gill-arch, the lowermost two or three rakers reduced.

Scales ctenoid ; lateral line with 30 (f.1), 31 (f.1), 32 (f.4) or 33 (f.6) scales ; cheek with 3 or 4 series ; 5–6½ scales between the lateral line and the dorsal fin origin ; 7 or 8 (rarely 6 or 9) between the pectoral and pelvic fin bases. Scales on the pectoral region small or, less frequently, moderate.

Fins. Dorsal with 24 (f.8) or 25 (f.4) rays, anal with 11 (f.4) or 12 (f.8), comprising XV or XVI, 9 or 10 and III,'8 or 9 spinous and branched rays for the fins respectively. Caudal truncate. Pectoral 72·5–92·0 (M = 80·2) per cent of head.

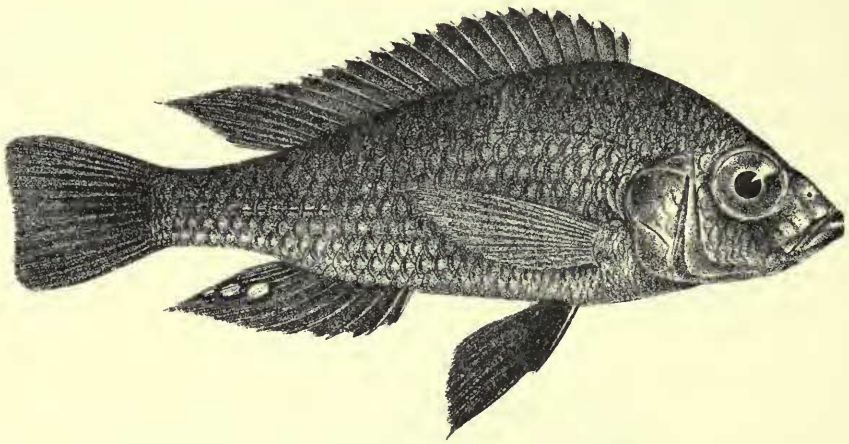

FIG. 7. *Haplochromis cinereus ;* holotype (from Boulenger, *Fishes of the Nile*).

Teeth. Teeth in the outer row of both jaws are weakly bicuspid or unicuspid, relatively stout and slightly recurved ; in most fishes there is an admixture of both types, with unicuspids predominating. There are 40–54 teeth in the upper, outer row.

The inner series are composed of either unicuspid or bicuspid teeth ; less commonly there is a mixture of both types. A characteristic feature of the inner tooth-rows is the way in which the teeth are implanted obliquely so that the crowns point posteriorly. Three or 4 (rarely 2) inner rows occur in the upper jaw and 2 or 3 in the lower.

The dentition of *H. cinereus* is unlike that of other species in the " generalized species " group ; it is, indeed, typical of the dentition found throughout the large group of piscivorous predators. However, in other characters (syncranial architecture, feeding habits and body-form) *H. cinereus* is one of the generalized species (see p. 242).

Lower pharyngeal bone triangular, the dentigerous surface slightly broader than long. Teeth in the two median rows are slightly enlarged in five of the specimens examined, but are slender in the remaining seven fishes; the other pharyngeal teeth are slender in all specimens.

Coloration in life unknown. *Colour of preserved fishes: Adult males.* Ground colour greyish-brown; chest and branchiostegal membrane dusky; a faint lachrymal stripe. All fins hyaline, with very faint indications of dark maculae on the soft dorsal; dorsal lappets dark. Anal fin with two or three whitish ocelli (orange surrounded by red in newly preserved material, according to Boulenger). Pelvics black except for a large light area extending over the distal half but not including the first branched ray. *Females.* Brownish, silvery grey ventrally, with eight or nine dark transverse bars on the flanks and caudal peduncle. All fins hyaline, the basal third to half of the caudal weakly maculate.

Distribution. Known only from Lake Victoria.

Ecology. No ecological data (except the locality) are available for the three specimens collected by Degen. The remaining nine fishes were caught in water less than 20 feet deep, over a sandy bottom on both protected and exposed shores.

Food. The stomach and intestinal contents of ten specimens (from four localities) were examined. Of these, three were empty and the remainder yielded sand-grains, bottom detritus (including fragments of plant epidermis) and some larvae of dipterous insects.

Breeding. The species is a female mouth-brooder. The smallest specimens available (a male and a female 71 mm. S.L.) are both sexually mature. As far as can be determined from this inadequate sample, both sexes reach the same adult size.

Discussion of affinities and synonymy. In Regan's revision of the Lake Victoria *Haplochromis* (1922) the definition of *H. cinereus* was expanded to embrace a number of small and generalized or near-generalized forms previously recognized as distinct species. The first attempt to prune this complex was Lohberger's resurrection of *H riponianus* (see p. 252). Now, with more specimens available and some knowledge of *Haplochromis* in nature, it is clear that Regan's definition of *H. cinereus* must be narrowed considerably and that a further two species (*H. lacrimosus* and *H. pallidus*) should be resurrected. Amongst the group of anatomically and trophically unspecialized *Haplochromis* in Lake Victoria, *H. cinereus* is unusual because of its oral dentition (see p. 240). Relatively stout, clearly bicuspid teeth in the outer series of the jaws and erect tricuspid inner teeth are usual in the generalized species. The dentition of *H. cinereus*, on the other hand, shows a marked tendency for slender, unicuspid teeth to predominate in the outer rows; the few bicuspid teeth present are weakly cuspidate. The inner teeth of *H. cinereus* are also atypical for the group in that the usual erect and tricuspid form is largely replaced by slender unicuspids implanted so as to point posteriorly. In fact, the dentition of *H. cinereus* is very like that of many predatory species. With so few specimens of *H. cinereus* known it is impossible to generalize on its feeding habits; however, the gut contents of

seven fishes from four different localities do not even hint at the species being a piscivorous predator.

At this point it should perhaps be stressed that my observations are confined to adult fishes 70–90 mm. long ; juveniles have still to be discovered.

Because " *Haplochromis cinereus* " had become something of a dumping ground for any small *Haplochromis* species or specimen, the published information (Graham, 1929) on distribution and habitats can no longer be considered reliable. I have examined " *H. cinereus* " material collected by Graham and find that none of these specimens is referable to *H. cinereus, sensu stricto.* The bulk of this material is of undescribed species and will be dealt with in subsequent papers. Thus, Graham's remark that " the species (*H. cinereus*) is therefore widely distributed except in the deepest part of the lake " and Brooks' (1950, p. 159) elaboration of these data do not apply to *H. cinereus* but rather to the whole species-complex of generalized, bottom feeding *Haplochromis* in the lake.

Haplochromis cinereus has been cited as representing the ancestral type from which the present species-flock could have evolved (Regan, 1922 ; Greenwood, 1951). For the reasons mentioned above this concept must be abandoned ; there are several other *Haplochromis* species still surviving in Lake Victoria which are structurally closer to the ancestral type, for example *H. lacrimosus, H. nubilus* or *H. pallidus.*

The particular affinities of *H. cinereus* are difficult to determine. In gross anatomy and appearance *H. cinereus* does not differ markedly from the majority of small *Haplochromis* ; only when its dentition is considered does the difference appear striking. Like so many members of the generalized group, *H. cinereus* seems to be an independent offshoot from one of the basic stocks.

In overall appearance and perhaps in at least some ecological requirements *Haplochromis macrops* is the one extant species most like *H. cinereus.* The two species are differentiated principally by the larger eye, shallower preorbital and the stouter, more numerous outer teeth of *H. macrops.*

Haplochromis cinereus is not, as Regan suggested, closely related to *H. ishmaeli.* To stress this supposed relationship, Regan noted that six of the *H. ishmaeli* syntypes were actually specimens of *H. cinereus.* As a result of this present revision none of these specimens is still retained in *H. cinereus. Haplochromis ishmaeli* belongs to a distinct phyletic line, discussed more fully on pages 269 and 273.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.292 (Holotype)	Buganga	Degen
B.M. (N.H.).—1906.5.30.350	Entebbe	,,
,, 1906.5.30.482	Bunjako	,,
,, 1959.4.28.41	Entebbe, Harbour	E.A.F.R.O.
,, 1959.4.28.48–50	Entebbe, Airport beach	,,
	Tanganyika	
,, 1959.4.28.42–47	Mwanza, Capri Bay	E.A.F.R.O.

Haplochromis niloticus nom. nov.
(Text-fig. 8)

Tilapia bayoni Boulenger, 1911, *Ann. Mus. Genova* (3), **5**; 72, pl. III, fig. 2 (*nec Paratilapia bayoni* [= *Haplochromis bayoni* (Blgr.), see Regan, 1922, p. 176] Blgr., 1909, *Ann. Mus. Genova* (3), **4**, 304, fig.
Haplochromis humilior (part), Regan, 1922, *Proc. zool. Soc. London*, 169.

Description, based on the holotype (100 mm. S.L.) and two other specimens 96 and 102 mm. S.L.

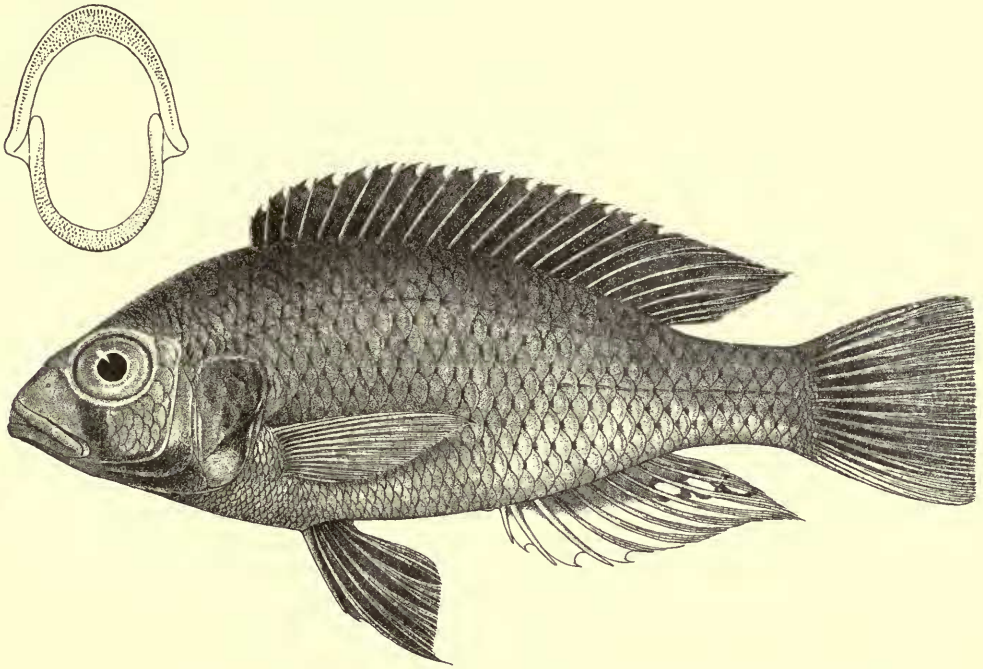

FIG. 8. *Haplochromis niloticus ;* holotype (from Boulenger, *Ann. Mus. Genova*).

The principal morphometric characters are given below :

S.L.	Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Ck. %	Lj. %	C.P.*
96·0	35·4	33·3	17·2	21·8	31·3	31·3	20·4	39·0	18·2
†100·0	33·0	33·0	15·2	24·3	30·3	33·5	24·0	33·3	17·5
102·0	34·3	33·8	17·4	24·7	29·0	30·5	23·2	37·7	17·1

† Holotype.
% Per cent. of head length.
* Per cent. of standard length.

Dorsal head profile sloping rather steeply (*ca.* 45°–50°) and slightly curved. Mouth horizontal ; jaws equal anteriorly, the length/breadth ratio of the lower 1·6–1·9. Posterior tip of the maxilla extending to the vertical through the anterior part of the eye. Lips not markedly thickened.

Gill rakers moderately stout ; 7 or 8 (the lowermost one or two reduced) on the lower part of the first arch.

Scales ctenoid ; 32 in the lateral line ; cheek with 2 or 3 series. Six or 7 scales between the lateral line and the dorsal fin origin, 8 or 9 between the pectoral and pelvic fin bases ; scales on the pectoral region small.

Fins. Dorsal with 25 (f.2) or 26 (f.1) rays, anal with 12, comprising XVI, 9–10 and III, 9 spinous and branched rays for the fins respectively. Pelvic fins with the first branched ray only slightly produced and extending to the origin of the anal. Caudal sub-truncate, scaled only on its proximal half.

Teeth. The outer row in both jaws is composed of moderately slender, movably implanted and unequally bicuspid teeth ; the most posterior five or six teeth in the upper jaw are caniniform and stouter than those situated anteriorly and laterally. There are 65–70 teeth in the upper, outer series.

Teeth in the inner series are small and tricuspid, and are arranged in four or five rows in the upper jaw and four in the lower. The interspace between the inner and outer series is very narrow.

Lower pharyngeal bone triangular, slender or slightly enlarged, the two median rows of teeth relatively coarse in two specimens (including the holotype) and somewhat more enlarged in the third. In the latter fish the next lateral row of teeth is also enlarged and the most posterior teeth of the median rows are sub-molariform.

Osteology. A complete skeleton was prepared from one of the specimens caught at the same time as the three fishes described above. However, since *H. niloticus* is very similar to *H. nuchisquamulatus* (which also occurs in the Victoria Nile) it is difficult to confirm the specific identity of the skeleton. Apparently the sole diagnostic osteological character is the lower pharyngeal bone, which is slender in *H. nuchisquamulatus* and slightly thickened in *H. niloticus*. The lower pharyngeal of the skeleton is that of *H. niloticus* and on this character alone the skeleton is referred to *H. niloticus*. In all other characters, except the oral dentition, the skeleton of *H. niloticus* resembles that of a generalized *Haplochromis* species. There are 14 + 16 vertebrae.

Coloration of live fishes is unknown. The three preserved specimens are all apparently males (judging from the well-defined anal ocelli) and adult. Because most of the coloration is now lost (the fishes are a uniform brownish-grey) I quote the description given by Boulenger (1911) of the then newly preserved specimens. " Back dark olive to blackish, sides brassy yellow to coppery red ; a more or less distinct black bar below the eye ; dorsal and ventrals brown to black ; anal pink, blackish at the base, usually with two or three large orange ocellar spots ; caudal brown or blackish the lower third often pink." From this description the coloration of male fishes seems to be remarkably like that of *H. humilior* from Lake Victoria (see p. 250).

Distribution. Haplochromis niloticus is known only from the Victoria Nile ; no information is available on its habitat or on feeding and breeding habits.

Affinities. Haplochromis niloticus has been compared with two *Haplochromis* species from Lake Victoria. In his original description, Boulenger compared the

species with *H. martini*, whilst Regan (1922) considered *H. niloticus* to be conspecific with *H. humilior*. In my opinion *H. martini* and *H. humilior* are not closely related to one another and *H. niloticus* is not allied to either. The three species differ in several fundamental characters, especially in the nature of their dentition. Admittedly, the somewhat enlarged median pharyngeal teeth of *H. niloticus* approach the condition found in some specimens of *H. humilior*, but the oral dentition of the two species is very dissimilar. The outer teeth are finer and more numerous in *H. niloticus* and there are more rows of inner teeth barely separated from the outer row. These same characters, together with a somewhat different arrangement of the jaw skeleton, serve to separate *H. niloticus* from *H. martini*.

The nature of the dentition in *H. niloticus* suggests affinity with *H. nigricans* and *H. nuchisquamulatus*, particularly the latter. From *H. nigricans*, *H. niloticus* is distinguished by its more generalized neurocranium and dentary (see Greenwood, 1956*b*) and its slightly enlarged lower pharyngeal teeth. From *H. nuchisquamulatus*, *H. niloticus* is again distinguished by having somewhat enlarged pharyngeal teeth and by a narrower interorbital region.

The affinities of *H. niloticus* are not especially obvious; the species is probably yet another slightly specialized side branch from the generalized *Haplochromis* stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12932) (Holotype *T. bayoni* Blgr. 1911)	Kakindu, Victoria Nile	Bayon
B.M. (N.H.).—1911.3.3.124–5	,, ,,	,,
,, 1911.3.3.126 (skeleton)	,, ,,	,,

Haplochromis martini (Blgr.) 1906
(Text-fig. 9)

Tilapia martini, Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 449.
T. martini (part), *Idem*, 1914, *Cat. Afr. Fish.* **3**, 239, fig. 158.
Haplochromis martini, Regan, 1922, *Proc. zool. Soc. London*, 171.

Regan (1922) based his redescription of *H. martini* on three of the six syntypes, but did not indicate to what species he referred the remaining type specimens. However, amongst the material Regan identified as *H. cinereus* there are three type specimens of *T. martini* (B.M. (N.H.) Reg. No. 1906.5.30.466–468). Presumably it was Regan's intention to include these in the published synonymy of *H. cinereus*. The three specimens are not *H. cinereus* but are, in fact, *Haplochromis martini*.

Lectotype. A brooding female 88 mm. standard length (B.M. (N.H.) Reg. No. 1906.5.30.465) from Bunjako, Uganda.

Description, based on twenty-nine specimens (including the lectotype and four paratypes) 59–104 mm. S.L.

Depth of body 30·8–38·0 (M = 34·4) per cent of standard length, length of head 31·0–38·1 (M = 35·4) per cent. Dorsal head profile very strongly decurved, the snout sloping at an angle of *ca.* 50°–70°. Depth of preorbital 13·0–20·0 (M = 16·6) per cent of head, least interorbital width 20·4–26·8 (M = 24·1) per cent. Snout slightly longer than broad, its length 27·3–34·4 (M = 30·2) per cent of head ; diameter of eye 29·4–37·5 (M = 31·7) per cent, depth of cheek 20·4–27·7 (M = 24·6) per cent. Caudal peduncle 15·3–20·6 (M = 17·3) per cent of standard length, 1·2–1·8 (mode 1·6) times as long as deep.

Jaws equal anteriorly, the lower 38·4–45·8 (M = 42·6) per cent of head, 1·6–2·1 (modal range 1·7–2·0) times as long as broad ; mouth horizontal or slightly oblique. Posterior tip of the maxilla extending to the vertical through the pupil or, less commonly, only to the anterior part of the eye. Such a marked posterior extension of the maxilla is unusual in Lake Victoria *Haplochromis* and may be considered one of the diagnostic characters of *H. martini*.

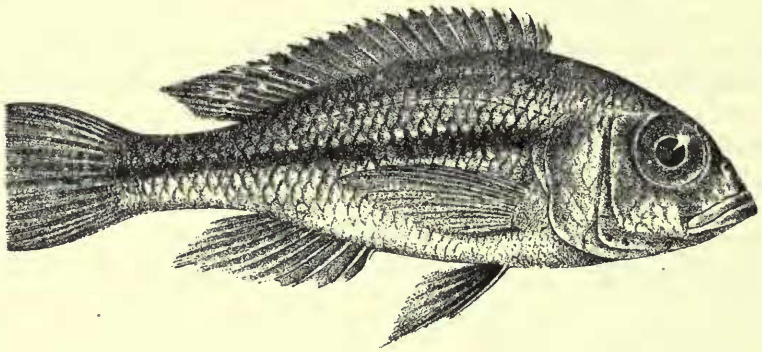

FIG. 9. *Haplochromis martini ;* lectotype (from Boulenger, *Fishes of the Nile*).

Gill rakers on the first arch moderately stout (but rather slender in a few specimens), one or two of the uppermost often flattened and bifid ; 8 or 9, rarely 7 or 10 (mode 9) gill rakers on the lower part of the arch.

Scales ctenoid ; lateral line with 31 (f.5), 32 (f.7), 33 (f.9), 34 (f.7) or 35 (f.1) scales ; cheek with 3 or 4 rows. Six to 8 scales between the lateral line and the dorsal fin origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.9), 25 (f.19) or 26 (f.1) rays, anal with 11 (f.8), 12 (f.19) or 13 (f.2), comprising XIV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral fin 73·5–86·5 (M = 82·0) per cent of head ; caudal truncate or sub-truncate.

Teeth. In the outer row of both jaws the teeth are slender and mainly unequally bicuspid in fishes less than 85 mm. S.L. Above this size both weakly bicuspid and unicuspid teeth occur together. In fishes of all sizes a few tricuspid teeth are found postero-laterally in the upper jaw, an uncommon character in Lake Victoria *Haplochromis* (see *H. macrops*, p. 237). There are 46–76 teeth in the upper jaw (ill-defined modal range 68–70).

Tricuspid teeth predominate in the inner series although in one large fish (101 mm. S.L.) the inner teeth are all unicuspid. The inner series are arranged in 2 (less commonly 3) rows in the upper jaw and in 1 or 2 (less commonly 3) rows in the lower.

Lower pharyngeal bone triangular, not enlarged and with slender, cuspidate teeth.

Osteology. The neurocranium does not differ greatly from the generalized *Haplochromis* type, but the premaxilla has relatively longer dentigerous arms.

Coloration in life. Sexually active males. Ground colour golden-yellow, shading to silvery-white, with three or four faint black blotches below the insertion of the dorsal fin, and a distinct coppery sheen on the nape and anterior part of the flank. Dorsal fin hyaline, with a pinkish flush. Distal half of the anal scarlet, the proximal half colourless ; anal ocelli orange-red. Caudal fin flushed with scarlet, especially intense on the distal half. Pelvics dark on the outer half, reddish-yellow mesially. *Quiescent males* golden-yellow shading to silvery-white ventrally ; a fairly distinct dark mid-lateral stripe and an interrupted upper stripe slightly below the insertion of the dorsal fin. Dorsal and caudal fins darkish, the anal and pelvics lighter ; anal ocelli yellow. *Females and juvenile males.* Ground colour and banding as above, the upper band usually broken into rather indistinct blotches. All fins light yellow, the caudal somewhat darker.

Preserved material. Both sexes. Ground colour yellowish-silver to brownish, an intense, narrow mid-lateral black line extends from the upper angle of the operculum to the caudal peduncle and, in some specimens even on to the caudal fin ; a fainter, often interrupted black stripe runs mid-way between the upper lateral line and the dorsal fin base. In some fishes there are traces of a very faint interocular band. All fins hyaline ; in males the dorsal has dusky lappets and the pelvics are dark.

Distribution. Haplochromis martini is known only from Lake Victoria. Specimens from Lake Edward once identified as *Tilapia martini* (Boulenger, 1914) were later referred to *H. schubotzi* (Regan, 1921).

Ecology. Habitat. Available records (from eight localities) suggest that *H. martini* is restricted to water less than 40 feet deep, where the species is ubiquitous but nowhere common. The species has been found over both sand and mud bottoms, on exposed shores and in sheltered bays. There are some indications that it may not occur close inshore since the only record of *H. martini* in beach-operated seine nets came from an area (Majita) where the nets were shot about 300 yards off-shore.

Food. Sixteen of the twenty-two specimens examined had ingested material in the stomach and intestines ; in three of these specimens, however, the contents were unidentifiable sludge. Eleven of the remaining thirteen fishes contained, as the exclusive or predominating food, the fragmentary remains of small fishes (identified in two cases as *Haplochromis*) ; one of these individuals had also fed on larval Diptera and another had eaten what appeared to be the foot and other soft parts of a snail. Another fish had fed only on larval Diptera and one was empty except for some small fish bones in the posterior intestine.

Breeding. *Haplochromis martini* is a female mouth-brooder ; females reach sexual maturity at *ca.* 80 mm. S.L. ; no data are available for males. Both sexes appear to attain the same maximum adult size.

Affinities. Because of its strongly decurved snout, large eye and the marked posterior extension of the premaxilla, *H. martini* is one of the more immediately recognizable species. Yet, despite these characters *H. martini* retains most of the fundamental features of a generalized species such as *H. macrops*. On the other hand, *H. martini* differs from members of this species group (and probably most other Lake Victoria species) in its bright yellow coloration.

When attempting to assess the phyletic affinities of *H. martini* one is faced with these rather contradictory characters and with the fact that, despite its generalized dentition and body-form, *H. martini* can be a piscivorous predator. The majority of piscivorous *Haplochromis* in Lake Victoria are larger than *H. martini* and have elongate bodies and heads ; the teeth in these species are usually large and caniniform.

Taking into account the various structural and ecological characters *H. martini* should perhaps be considered a superficially but trophically distinct branch from the generalized stem as represented, perhaps, by an *H. macrops*-like ancestor.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.463–5 (Lectotype and paratypes)	Bunjako	Degen
,, 1906.5.30.466–8 (Paratypes)	,,	,,
,, 1959.4.28.124–132	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.138	Old Bukakata Bay	,,
,, 1959.4.28.140	Napoleon Gulf, near Jinja	,,
	Tanganyika	
,, 1959.4.28.116–123	Majita	,,
	Kenya	
,, 1959.4.28.133–137	Off Port Southby	,,
,, 1959.4.28.139	Beach below Usoma Lighthouse	,,

Haplochromis humilior (Blgr.) 1911

(Text-figs. 10 and 11)

Tilapia humilior Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 74, pl. III, fig. 3.
Tilapia lacrimosa (part), Boulenger, 1915, *Cat. Afr. Fish.* **3**, 234.
Haplochromis desfontainesii (part), Boulenger, 1915, *tom. cit.*, 303.
Haplochromis nubilus (part), Regan, 1922, *Proc. zool. Soc. London*, 164.
Haplochromis humilior (part), Regan, 1922, *op. cit.*, 169.
? Paratilapia granti (part), Boulenger, 1915, *tom. cit.*, 342.

Lectotype. A male 90 mm. standard length from Kakindu, Victoria Nile, collected by Bayon (now in the collections of the Museo Civico di Storia Naturale, Genoa).

Description, based on thirty specimens 65–90 mm. S.L. (including the lectotype and one paratype; the second paratype [B.M. (N.H.) Reg. No. 1911.3.3.152] is very poorly preserved and although examined, is not included in the description).

Depth of body 29·0–37·5 (M = 34·4) per cent of standard length, length of head 31·6–37·8 (M = 34·7) per cent. Dorsal head profile curved, sloping at an angle of 45°–50°. Preorbital depth 13·6–17·9 (M = 16·3) per cent of head, least interorbital width 21·0–28·6 (M = 24·2) per cent. Snout as long as broad or slightly longer, its length 27·0–34·8 (M = 30·9) per cent of head, diameter of eye 27·0–32·5 (M = 30·3), depth of cheek 18·5–23·2 (M = 21·2) per cent. Caudal peduncle 15·2–19·1 (M = 17·4) per cent of standard length, 1·3–1·8 (mode 1·5) times as long as deep.

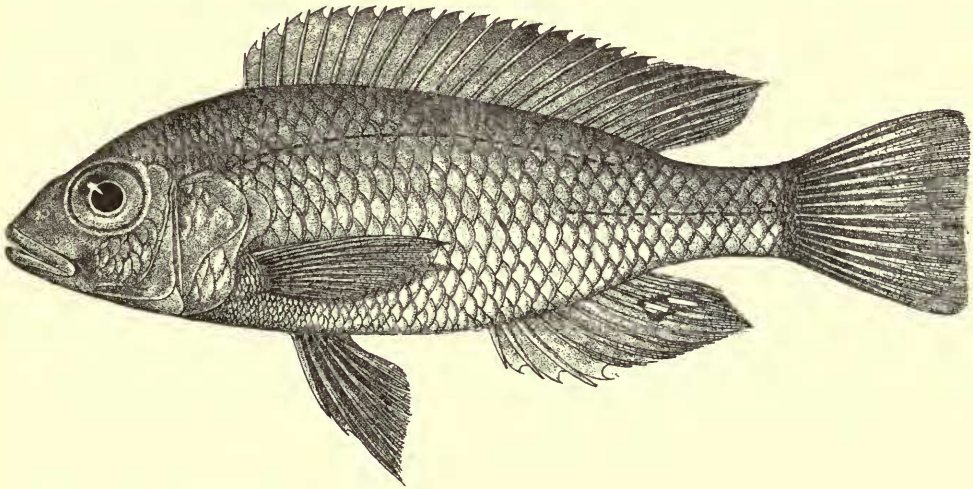

FIG. 10. *Haplochromis humilior,* lectotype (from Boulenger, *Ann. Mus. Genova*).

Mouth horizontal, the lower jaw often slightly shorter than the upper; length of lower jaw 33·4–39·6 (M = 36·6) per cent of head and 1·3–2·2 (modal range 1·5–1·8) times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or somewhat beyond (to below the pupil in one specimen).

Populations of *H. humilior* from different localities in the lake appear to have characteristic facies which make any one population more or less readily identifiable; unfortunately no means of quantifying these characters could be determined. Also, it has so far proved impossible, through lack of material, to decide whether Lake Victoria *H. humilior* differ from those inhabiting the Victoria Nile.

Gill rakers short and stout, 6–8 (modes 6 and 7), rarely 9 on the lower part of the first arch.

Scales ctenoid; lateral line with 30 (f.7), 31 (f.7), 32 (f.7) or 33 (f.7) scales; cheek with 2 or 3 (rarely 4) series. Six or 7 scales between the lateral line and the origin

of the dorsal fin, 6–8 (rarely 5 or 9) between the pectoral and pelvic fin bases. Scales on the pectoral region relatively small.

Fins. Dorsal with 24 (f.6), 25 (f.21) or 26 (f.3) rays, anal with 11 (f.4) or 12 (f.24) comprising XV–XVI, 8–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral 69·0–92·3 (M = 81·0) per cent of head. Caudal truncate.

Teeth. The outer teeth in both jaws are moderately stout and unequally or, less frequently, sub-equally bicuspid. In fishes over 70 mm. S.L. some weakly bicuspid or even unicuspid teeth may occur; there are 36–52 (modal range 46–48) teeth in the upper, outer series.

Inner teeth are tricuspid and arranged in 2 or 3 (rarely 4) rows in the upper jaw and 1 or 2 (rarely 4) in the lower. A distinct space separates the inner and outer tooth series.

Lower pharyngeal bone and teeth. The lower pharyngeal bone, although relatively stout is less massive than the bone in a specimen of *H. ishmaeli* or *H. pharyngomylus*

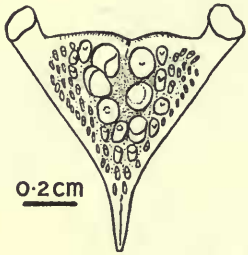

FIG. 11. *Haplochromis humilior*; lower pharyngeal bone, occlusal view, from a Lake Victoria specimen.

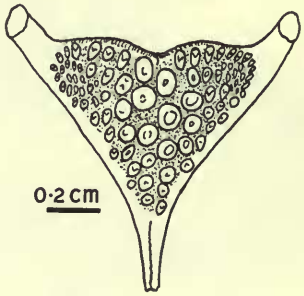

FIG. 12. *Haplochromis theliodon*; lower pharyngeal bone, occlusal view.

of the same size. Teeth in the two median rows are always enlarged, with the most posterior one or two pairs largest. There is some variation in the degree of enlargement of the median teeth, which may be bicuspid, conical or even molariform; no clear-cut correlation could be detected between, on the one hand, tooth-size and form and, on the other, the sex and size of the fish. There is, however, a tendency for larger individuals to have the coarsest median pharyngeal teeth. Sagittal sections through a number of bones (from fishes 65–70 mm. S.L.) suggest that both time and chance may influence the nature of the dentition, since unerupted replacement teeth are always molariform irrespective of the nature of the functional teeth which they underlie.

In addition to the two median rows, the next lateral row on each side may also contain a number of molariform teeth.

Coloration in life. Breeding males. Ground colour dark silvery-grey with intense dusky blotches on the head; branchiostegal membrane dull black. A coppery flush extends over the cheek, operculum and flank as far as the origin of the anal fin. Anal and caudal fins light red, the colour becoming more intense along the

margins of both fins and the upper and lower posterior angles of the caudal ; two or three yellow anal ocelli. Dorsal fin dusky, with an orange-red margin to the soft part and red spots and bars between the rays of the posterior half of the spinous dorsal and over the entire soft part. Pelvics black. *Quiescent males.* General coloration as in females except that the pelvics are somewhat dusky and the unpaired fins have a pinkish flush ; anal ocelli are present. *Females.* Ground colour silvery-yellow. Dorsal, pelvic and anal fins pale yellow, the dorsal with red spots distributed as in males.

Colour of preserved material. Males. Greyish, darker dorsally, the chest and branchiostegal membrane sooty ; in some specimens there are traces of seven or eight, narrow transverse bars on the flank and caudal peduncle. A lachrymal stripe, a pair of transverse stripes across the snout and, in some fishes, a broad band across the interorbital region are also visible, as are one or two bands on the nape. Dorsal fin variable, from hyaline to dusky. Anal hyaline in quiescent fishes and whitish in active individuals. Pelvics black (darkest in active fishes) but with a whitish overlay on the proximal half. *Females* silvery, some with very faint traces of vertical bars usually most obvious on the mid-lateral aspects of the flanks. All fins hyaline.

Distribution. The species occurs in Lake Victoria and the Victoria Nile.

Ecology. Habitat. In Lake Victoria the species is confined to shallow water over sandy beaches in both exposed and sheltered areas. No data are available for the riverine populations.

Food. The gut contents of thirty-two fishes (from two localities) yielded identifiable material. Of these specimens, twenty-four contained bottom debris (sand grains, plant fragments, diatom frustules and blue-green algae) together with remains of both larval and pupal insects (especially Diptera and Trichoptera, less frequently, Ephemeroptera) ; four fishes contained only insect remains and one only the diatom *Melosira.* Ten individuals had eaten, in addition to insects, both bivalves (unidentifiable) and gastropods (*Melanoides* sp. and *Bellamya* sp.). These molluscan fragments were too finely divided to allow for any estimate of the number of animals eaten. Nevertheless it does seem, from this sample at least, that Mollusca are not a major element in the food of *H. humilior.*

The large quantities of sand found with the remains of Trichoptera larvae in most fishes is of interest, particularly since the grains are small and of a remarkably uniform size. This suggests that the sand grains could be derived from the sand-grain cases made by certain caddis larvae. The moderately large pharyngeal mill of *H. humilior* may thus serve the dual purpose of crushing mollusc shells and the sand-grain cases of certain larval insects.

Breeding. Nothing is known about the breeding habits of *H. humilior.* The smallest specimens available (a male and a female both 65 mm. S.L.) are adult ; the sexes apparently do not differ in maximum adult size attained.

Affinities. Haplochromis humilior differs from the generality of small *Haplochromis* species in several characters, particularly in having a relatively massive lower

pharyngeal bone and in having a low modal number of gill rakers (6–7). Another pronounced difference lies in the tendency for the lower jaw to be shorter than the upper. In most other characters, *H. humilior* resembles *H. pallidus*, a species which shows incipient hypertrophy of the lower pharyngeal bone. *Haplochromis humilior* could be a more specialized off-shoot from an *H. pallidus*-like stem. Unlike many other presumed phyletic lines within the Victoria species flock, this one is not continued by one or more extant species. *Haplochromis humilior* does not appear to have any close relationship to the principal group of species with enlarged pharyngeals, namely *H. obtusidens*, *H. ishmaeli* and *H. pharyngomylus*.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12910) (Lectotype)	Kakindu, Victoria Nile	Bayon
B.M. (N.H.).—1911.3.3.152–3 (Paratypes)	,, ,,	,,
,, 1906.5.20.314	Entebbe	Degen
,, 1959.4.28.88–107	Beach near Nasu Point	E.A.F.R.O.
,, 1959.4.28.108	Near Grant Bay	,,
,, 1959.4.28.109–112	Entebbe, Harbour	,,
	Tanganyika	
,, 1959.4.28.113–115	Majita	,,
	Kenya	
,, 1909.11.15.38	Kisumu Bay	Blayney-Percival

Haplochromis riponianus (Blgr.) 1911
(Text-figs. 4 and 13)

Pelmatochromis riponianus (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 69, pl. II, fig. 3; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 411, fig. 280.
Haplochromis riponianus, Lohberger, 1929, *Zool. Anz.* **86**, 222.
Paratilapia serranus (part), Boulenger, 1915, *tom. cit.*, 334.
Paratilapia victoriana (part), Boulenger, 1915, *tom. cit.*, 341.
Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446; *Idem*, 1915, *tom. cit.* 293.
Haplochromis cinereus (part), Regan, 1922, *Proc. zool. Soc. London*, 166.

On the basis of specimens in the Vienna Museum, Lohberger (1929) decided that Regan's views on the conspecificity of *Pelmatochromis riponianus* and *H. cinereus* could not be substantiated; consequently he resurrected the former species as *Haplochromis riponianus*. I have not examined Lohberger's specimens but, from studying considerably more material than was available to either Regan or Lohberger, I can fully endorse the latter's action.

Lectotype. A male 95·5 mm. standard length, from Jinja, Uganda, collected by Bayon (Genoa Museum, C.E. 12996).

Description, based on twenty-eight specimens (including the lectotype and two paratypes) 57–104 mm. S.L. One other paratype (B.M. (N.H.) Reg. No. 1911. 3.3.37) is not included in the description.

Depth of body 33·3–39·4 (M = 35·7) per cent of standard length, length of head 32·8–37·7 (M = 35·7) per cent. Dorsal head profile straight or very slightly curved, sloping at an angle of *ca.* 35°–45°. Preorbital depth 16·3–19·5 (M = 17·6) per cent of head, least interorbital width 23·0–28·1 (M = 25·1) per cent. Snout slightly longer than broad, its length 30·5–35·4 (M = 33·6) per cent of head ; diameter of eye 24·2–31·0 (M = 26·6), depth of cheek 19·2–25·0 (M = 22·7) per cent. Caudal peduncle 14·4–18·4 per cent of standard length, 1·2–1·7 times as long as deep (modal range 1·3–1·5).

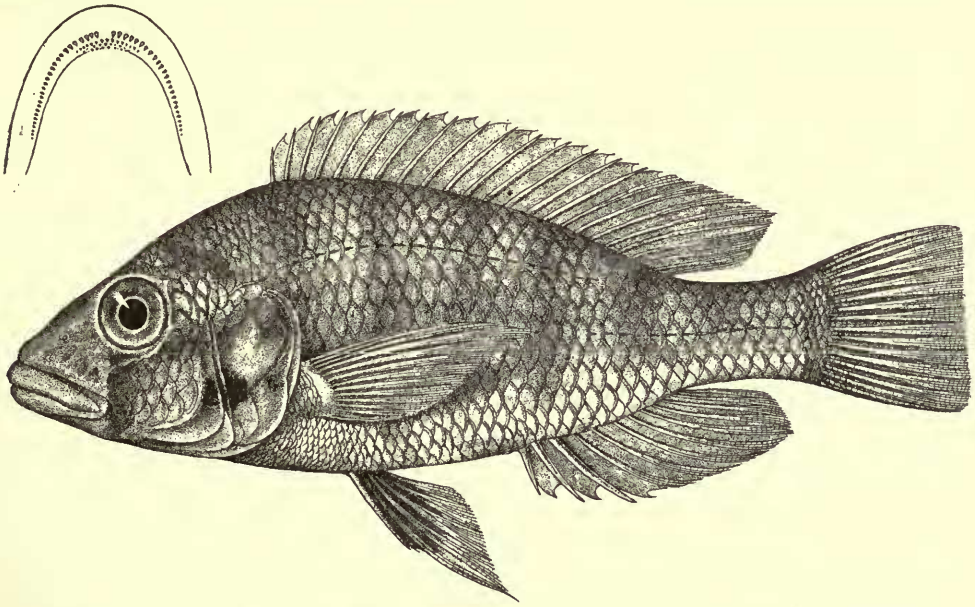

FIG. 13. *Haplochromis riponianus ;* lectotype (from Boulenger, *Ann. Mus. Genova*).

Mouth horizontal or very slightly oblique, jaws equal anteriorly, the lower 33·4–42·2 (M = 38·5) per cent of head and 1·3–2·0 (modal range 1·6–1·8) times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or almost so, occasionally to below the anterior quarter of the eye. Lips noticeably thickened but not produced into median lobes.

Gill rakers on the first arch moderately stout in most fishes but slender in a few others, the lowermost one to three reduced and the pair nearest the epi-ceratobranchial angle often flattened and tri- or quadrifid ; 6–8 (mode 7) rakers on the lower part of the arch.

Scales ctenoid ; lateral line with 30 (f.2), 31 (f.2), 32 (f.11), 33 (f.10) or 34 (f.2) scales, cheek with 3 or 4 series ; $5\frac{1}{2}$-7 (rarely 5 or 8) scales between the lateral line and the dorsal fin origin ; 7 or 8 (rarely 6) between the pectoral and pelvic fin bases. Scales on the pectoral region moderate.

Fins. Dorsal with 24 (f.3), 25 (f.24) or 26 (f.1) rays, anal with 11 (f.3) or 12 (f.25), comprising XV–XVI, 9–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral 69·0–88·5 (M = 78·5) per cent of head. Caudal sub-truncate.

Teeth. The outer teeth in both jaws are relatively slender and slightly to strongly recurved; the basic cusp pattern is unequally bicuspid, but the crowns are often so worn that the teeth appear to be weakly cuspidate or even unicuspid and bluntly incisiform. In some fishes over 80 mm. S.L. initially unicuspid teeth occur and may even be the predominating form in fishes more than 100 mm. S.L. The number of teeth in the upper, outer rows shows slight positive allometry with standard length; there are 38–62 teeth in this row.

Unicuspid and weakly tricuspid teeth are found in the inner rows; often both types of teeth occur together, especially in fishes over 80 mm. S.L. The inner teeth are implanted at an angle and may be buried in the thickened oral mucosa (possibly a preservation artefact). In the upper jaw, the inner teeth are arranged in 3 or 4 (rarely 2) rows and in the lower in 2–4 (rarely 1) rows.

Boulenger's description (1911 and 1915) of the inner teeth as " minute " appears to stem from his being misled by the thickened oral epithelium which has hidden all but the tips of these teeth.

Lower pharyngeal bone and teeth. The lower pharyngeal bone is triangular and in most specimens fairly stout. The relative degree to which the bone is enlarged is somewhat greater than that of the lower pharyngeal in *H. humilior* (see p. 250). In a few fishes, however, the bone is slender. This variation in stoutness is not entirely correlated with size since, although the smallest specimens have slender or but slightly thickened bones, some of the larger fishes do not have proportionately enlarged pharyngeals.

The form of the teeth in the four median rows does show correlation with both the size of the individual and the stoutness of the bone. In fishes less than *ca.* 70 mm. S.L. some of the posterior teeth in the two median rows are enlarged; in fishes 70–80 mm. most of the median teeth are enlarged as are some or all of the teeth in the row on each side of the two median rows. Next, in specimens above 80 mm. S.L. (except those with slender pharyngeal bones) the teeth of these four rows are larger still, whilst those in the two median rows tend to be molariform. Finally, in fishes over 98 mm. S.L. some of the more lateral teeth are also molariform. Large individuals with slender lower pharyngeals have only slightly enlarged median teeth, comparable with those of the smaller (< 90 mm.) specimens described above.

Osteology. The shape of the neurocranium departs from the generalized type towards the form found in the elongated, piscivorous predators (as typified by *H. mento*). In *H. riponianus*, the slope from the anterior tip of the vomer to the base of the supraoccipital crest is less steep and more nearly straight than in the generalized type of skull; also, the preorbital region in *H. riponianus* is relatively longer than in, for example, the skull of *H. obliquidens* or *H. macrops*.

Coloration. The colours of live fishes are unknown.

Preserved material. Sexually active males. Ground colour greyish-brown, chest dusky; a dark lachrymal stripe and faint traces of four interrupted transverse bars on the flanks. Dorsal, caudal and anal fins hyaline, the anal with two or three

dead-white ocelli, usually arranged in a single row, but occasionally in two rows. Pelvic fins black. *Immature males* similar to females but with darker pelvics and small, distinct ocelli on the anal fin. *Females* silvery-grey shading to silver ventrally ; six to ten transverse bars of variable width (narrowest when most numerous) across the flanks and caudal peduncle ; sometimes, a very faint lachrymal stripe. All fins hyaline, the caudal occasionally maculate ; in a few specimens there are one or two, small, dead-white spots in the same position as the ocelli on the anal fin of males.

Distribution. Lake Victoria and possibly the Victoria Nile. The latter locality is surmised from the data given in the original description of the species. In that paper (Boulenger, 1911), the locality is given only as Jinja, Ripon Falls, but in the introduction Boulenger implies that the entire collection, of which *H. riponianus* formed part, was from the Victoria Nile, that is *below* the Ripon Falls. Later (*Cat. Afr. Fish.* **3**, 1914) the type-locality is given more specifically as " Ripon Falls, Victoria Nile."

Ecology. Habitat. The species is apparently confined to sand or rock substrates in the littoral regions of the lake ; it has been caught in both exposed and sheltered localities.

Food. Stomach and intestinal contents of thirty-two fishes (from one locality) show that at least this population of *H. riponianus* was mainly insectivorous, although some fishes had also fed on Mollusca. Insect larvae (especially Trichoptera and Ephemeroptera) were found in every fish. As in *H. humilior* (see p. 251) large quantities of uniformly sized sand-grains were found in the intestines of most fishes. Since these grains closely resemble those forming the cases of certain Caddis-fly larvae found intact in some individuals, it is suggested that the sand was derived, at least partly, from crushed cases. In addition to the main contents listed above, eight fishes contained relatively large quantities of crushed bivalve shells (? *Corbicula* sp.) ; a few fragments of gastropod shells were also found in these individuals.

Breeding. No information is available on the breeding habits of *H. riponianus*. The smallest sexually mature fish is a female 84 mm. S.L. ; the smallest adult male is 86 mm. S.L.

Affinities. In combination, the oral and pharyngeal dentition set *H. riponianus* apart from other Lake Victoria species. In appearance and in possessing a similar oral dentition, *H. saxicola* (see p. 257) appears to be the nearest relative of *H. riponianus* although it differs in having a relatively slender pharyngeal bone with only the two median tooth rows slightly enlarged. The two species, which differ somewhat in their ecological relationships, may represent separate adaptive lines derived from a common ancestor.

Haplochromis pallidus seems structurally suited for consideration as the extant representative of the presumed ancestor. (See also p. 235.)

Although the lower pharyngeal bone and its dentition are similar in *H. humilior* and *H. riponianus* and although both species have very similar ecological require-

ments, the species show quite marked divergence in body-form (especially head shape) and oral dentition. What relationships there are probably lie far back in their phylogenetic history; certainly the two species cannot be considered members of a recently evolved phyletic line.

Boulenger's view (1911) that *H. riponianus* and *H. microdon* are closely related can no longer be held; the two species have very different phylogenies, as witnessed by several anatomical and osteological characters, and equally distinctive habits (Greenwood, 1959). Boulenger was undoubtedly misled by the supposedly small teeth of both species (Greenwood, op. cit., and above) whereas in fact the teeth of *H. riponianus* are not minute and are of a markedly different form from those of *H. microdon*.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12996 (Lectotype)	Jinja, Ripon Falls	Bayon
B.M. (N.H.).—1911.3.3.37–39	,, ,,	,,
,, 1911.3.3.24	,, ,,	,,
,, 1906.5.30.280	Entebbe	Degen
,, 1906.5.30.394 (Paratype *H. ishmaeli*)	Bunjako	,,
,, 1929.8.13.1	Entebbe	Hoare
,, 1959.4.28.141–157	Entebbe, Airport beach	E.A.F.R.O.
,, 1959.4.28.158	Hannington Bay	,,
,, 1959.4.28.159	Buka Bay	,,
,, 1959.4.28.160–162	Entebbe, Harbour	,,
	Lake Victoria, Locality Unknown	
,, 1901.6.24.86–87	—	Sir H. Johnson
,, 1928.5.24.136–138	—	M. Graham

Haplochromis saxicola,, sp. nov.
(Text-figs. 5 and 14)

Pelmatochromis riponianus (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 69; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 411.
Haplochromis cinereus (part) Regan, 1922, *Proc. zool. Soc. London*, 166.

Holotype. A female 111·0 + 25·0 mm. long (B.M. (N.H.) Reg. No. 1959.4.28.249) from Ramafuta island, Uganda.

Description, based on twenty-seven specimens (including the holotype of the species and two paratypes of *Pelmatochromis riponianus*) 106–123 mm. S.L.

Depth of body 34·8–42·5 (M = 37·8) per cent of standard length, length of head 35·3–42·5 (M = 37·8) per cent. Dorsal head profile straight or gently curved, sloping at *ca.* 30°–40°. Preorbital depth 15·2–19·0 (M = 17·6) per cent of head,

least interorbital width 23·9–29·8 (M = 26·9) per cent. Snout slightly longer than broad or, less commonly, as long as broad, its length 34·0–41·8 (M = 37·5) per cent of head ; diameter of eye 20·4–26·8 (M = 24·4), depth of cheek 21·4–26·2 (M = 23·9) per cent. Caudal peduncle 13·1–17·7 (M = 15·4) per cent of standard length, 1·0–1·5 (mode 1·3) times as long as deep.

Mouth horizontal or very slightly oblique ; lips variably thickened but always noticeably enlarged. Lower jaw 39·7–46·5 (M = 43·0) per cent of head and 1·5–1·9 (mode 1·8) times as long as broad. Posterior tip of the maxilla reaching or almost reaching the vertical through the anterior orbital margin, sometimes extending to below the eye.

Gill rakers moderately stout, the uppermost two or three either slender or divided

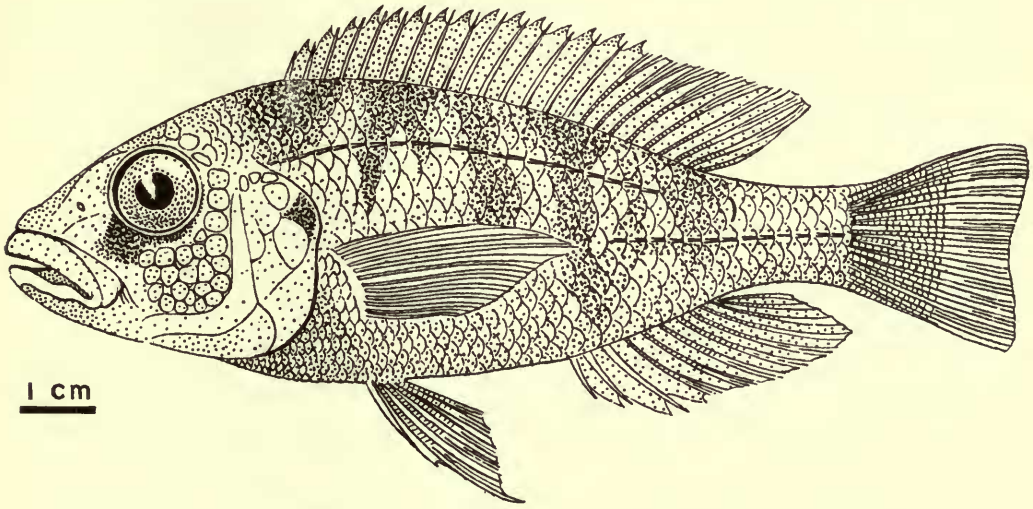

Fig. 14. *Haplochromis saxicola ;* holotype. Drawn by John Norris Wood.

and somewhat flattened, the lowermost one to three usually reduced ; 7–9 (mode 8) rarely 6 on the lower part of the first arch.

Scales ctenoid ; 31 (f.2), 32 (f.15), 33 (f.9) or 34 (f.1) in the lateral line ; cheek with 3 or 4 series. Six or 7 (rarely 5) between the lateral line and the dorsal fin origin ; 6–8 (rarely 5 or 9) between the pectoral and pelvic fin bases. Scales on the pectoral region small.

Fins. Dorsal with 24 (f.4), 25 (f.20) or 26 (f.2) rays, anal with 11 (f.1), 12 (f.24) or 13 (f.1), comprising XIV–XVI, 9 or 10 and III, 8–10 spinous and branched rays for the fins respectively. One specimen has XVI, 6 rays in the dorsal and another II, 8 in the anal. Pectoral 67·8–81·0 (M = 74·5) per cent of head. Caudal truncate or sub-truncate.

Teeth. In the outer series of each jaw the teeth are slender, recurved and generally unicuspid, but a few weakly bicuspid teeth may occur in fishes less than 115 mm. S.L.

The crowns of the teeth are often worn so as to assume a bluntly incisiform shape. There are 52–68 teeth in the outer row of the upper jaw (modal range 60–62).

The inner tooth rows are composed of obliquely implanted and either unicuspid or both uni- and tricuspid teeth arranged in 2 or 3 (rarely 4 or 5) rows in each jaw.

The dentition of *H. saxicola* bears a very strong resemblance to that of *H. riponianus*, the major difference lying in the higher percentage of primarily unicuspid teeth in *H. saxicola*. However, it must be borne in mind that no available specimens of *H. riponianus* are as large as even the smallest *H. saxicola*.

Lower pharyngeal bone and teeth. In ninety per cent of specimens examined, the lower pharyngeal bone is not enlarged ; in the remaining ten per cent it is somewhat thickened and resembles the lower pharyngeal of *H. riponianus*.

The two median tooth rows are slightly enlarged in all specimens and may even be molariform in those individuals with enlarged lower pharyngeal bones. Very exceptionally, the median teeth are not noticeably larger than the more lateral ones.

Osteology. The neurocranium of *H. saxicola* is very like that of *H. riponianus* (see p. 254) ; the premaxilla is, however, distinctive for its noticeably arched dentigerous arms which impart a characteristic peak to the antero-medial part of the bone.

Coloration in life. Sexually active males. Ground colour dark grey-green, some scales on the flank with golden centres ; chest and branchiostegal membrane black ; a coppery-red flush on the operculum and flanks. Dorsal fin dark, lappets and maculae red ; caudal blue-grey with red posterior and ventral margins ; anal fin blue-grey, suffused with pink, especially the distal margins, ocelli bright yellow ; pelvic fins black. *Quiescent males* pale silvery-blue, almost grey dorsally ; some flank scales with golden centres, pectoral region silver. Dorsal, caudal and pelvic fins hyaline, the dorsal with pale red lappets and margin to the soft part, pelvics dusky on the lateral half, hyaline mesially. *Females.* Ground colour golden-grey ; all fins hyaline.

Preserved material. Adult males (probably sexually active). Ground coloration dark grey-black, especially dark on the head, dorsal aspects of the flanks and along the ventral body surface. Lips light grey ; branchiostegal membrane black. Dorsal fin dark, with light maculae on the soft part. Anal fin black on the basal third, the distal two-thirds yellowish, with two grey ocelli. Caudal greyish ventrally, yellow around the margin.

Females, juvenile and some apparently adult (? quiescent) males. Brownish-yellow ground coloration, darkest on the dorsal surface of the head ; four to seven, fairly narrow dark transverse bars on the flanks and caudal peduncle. Dorsal and caudal fins greyish, all other fins colourless, except for the black pelvics in adult males.

Distribution. The species is known definitely from Lake Victoria but may also occur in the Victoria Nile. This locality is suggested by the presumed provenance of two *P. riponianus* paratypes now considered to be *H. saxicola*. For further discussion, see under " Distribution " in *H. riponianus*, p. 255.

Ecology. Habitat. The habitats in which *H. saxicola* has been caught are rather more varied than is common for most Lake Victoria *Haplochromis*. The species

occurs in shallow water over exposed sand or shingle beaches, amongst dense plant stands near rocky shores and over shingle and small boulders in water 10–30 feet deep. Finally, one specimen was caught more than a mile off-shore in nets set on a mud bottom in water *ca.* 180 feet deep. The most consistent factors in all these habitats (except the latter) are the hard substrates of sand, rock or shingle.

Food. Twenty-six fishes (from nine different localities) were examined; of these, only twelve contained any ingested material in the stomach or intestine. Sand grains and small pebbles (*ca.* 2 mm. in diameter) were found in eleven individuals; fragmentary insect larvae (Diptera, probably chironomids) formed the principal food in eight fishes and snails in one other. All specimens contained a few fragmentary Ostracoda and one, an almost entire larva of the boring May-fly *Povilla adusta*.

These very unsatisfactory data suggest that *H. saxicola* is a bottom feeder which preys on various invertebrates, particularly insect larvae.

Breeding. No information was obtained on the breeding habits of *H. saxicola*; the smallest specimen (106 mm. S.L.) is sexually mature. Both sexes appear to reach the same maximum adult size.

Affinities. In general appearance, oral dentition, neurocranial morphology and in certain ecological characters, *Haplochromis saxicola* closely resembles *H. riponianus*. The most striking difference between the species is the typically slender lower pharyngeal bone of *H. saxicola* and the stouter pharyngeal bone and teeth of *H. riponianus*. The mean snout and lower jaw proportional lengths for *H. saxicola* are somewhat greater than those for *H. riponianus*. If, however, these characters are taken for both species and plotted against standard length, no marked discontinuity is observed; in all morphometric characters *H. saxicola* could well be large *H. riponianus*.

The differences in the lower pharyngeal bones and dentition, however, are against this interpretation, the more slender bone with but slightly enlarged median teeth characterizing the larger specimens described as *H. saxicola*. In no *Haplochromis* species with enlarged pharyngeals does the bone and its dentition become less coarse with growth. Indeed, the reverse is usual (see Greenwood, 1959 and p. 277).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1959.4.28.249 (Holotype)	Ramafuta Isl.	E.A.F.R.O.
,, 1911.3.3.39 (Paratype of *Pelmatochromis riponianus*)	Jinja, Ripon Falls	Bayon
Genoa Museum (A paratype of *P. riponianus*)	,, ,,	Bayon
B.M. (N.H.).—1959.4.28.250–255	Ramafuta Island	E.A.F.R.O.
,, 1959.4.28.256–267	,, ,,	,,
,, 1959.4.28.268–270	Beach near Nasu Point	,,
,, 1959.4.28.271–272	Jinja	,,
,, 1959.4.28.273	0° 4′ S., 33° 14′ E.	,,

Haplochromis theliodon sp. nov.
(Text-figs. 12 and 15)

Holotype. A fish 95·0 + 20·0 mm. long (B.M. (N.H.) Reg. No. 1959.4.28.163) from Majita, Tanganyika Territory.

Description, based on seven specimens (including the holotype) 79–95 mm. S.L. The principle morphometric characters are summarized below:

S.L.	Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Ck. %	L.j. %	C.P.*
75·0	37·3	37·3	17·9	25·0	32·2	25·0	21·4	39·3	15·3
84·0	35·7	36·9	16·2	25·8	32·2	26·8	25·8	38·7	14·3
85·0	36·6	36·6	16·1	22·6	35·5	24·2	22·6	38·7	15·4
86·0	38·4	33·7	17·3	24·1	33·5	24·1	24·1	38·0	15·1
88·0	38·6	36·3	18·1	25·0	34·4	25·0	24·4	37·4	14·8
89·0	38·2	36·5	18·5	24·6	33·8	24·6	27·0	38·4	15·2
95·0	36·8	33·7	17·2	25·0	34·4	26·6	25·0	39·0	13·7

* Per cent. of standard length.
% Per cent. of head length.

Dorsal head profile straight except for a slight concavity above the eye, sloping fairly steeply; snout longer than broad. Mouth slightly oblique; lips, especially the upper, thickened. Lower jaw 1·5–1·8 times as long as broad. Posterior tip of the maxilla almost reaching the vertical to the anterior orbital margin.

Gill rakers variable, from stout (the commonest) to relatively slender; 7 (f.1), 8 (f.5) or 9 (f.1) on the lower part of the first arch. The lowermost two to four rakers may be reduced.

Scales ctenoid; lateral line with 31 (f.2), 32 (f.3) or 33 (f.2) scales; cheek with 3 or 4 series. Six to 9 scales between the lateral line and the dorsal fin origin, 7–9 between the bases of the pectoral and pelvic fins. Scales on the pectoral region small and deeply embedded.

Fins. Dorsal with 25 rays, anal with 12, comprising XV–XVI, 9 or 10 and III, 9 spinous and branched rays for the fins respectively. Pectoral 64·3–72·0 (M = 69·5) per cent of head. Caudal truncate or sub-truncate.

Teeth. In six of the seven specimens examined, the outer row in both jaws is composed of relatively stout, unequally bicuspid teeth, except for the most posterior pair in the upper jaw which are unicuspid. In the seventh specimen, the anterior and postero-lateral teeth are unicuspid and the lateral teeth unequally bicuspid. There are 36–46 outer teeth in the upper jaw.

The inner teeth are small and tricuspid (with a few unicuspids in the exceptional specimen mentioned above) and are arranged in 3 or 4 rows in the upper jaw and 3 or 4 (rarely 2) in the lower. Inner teeth are implanted vertically or somewhat obliquely.

Lower pharyngeal bone and teeth. The lower pharyngeal bone is thickened and moderately stout; that is to say, it is comparable with the lower pharyngeal in most *H. humilior* but finer than that in *H. obtusidens* (see p. 267).

Five of the seven specimens examined have the four median tooth rows composed of large and molariform teeth, whilst the next lateral row of each side contains enlarged but clearly cuspidate teeth. In the exceptional fishes, only the median pair of tooth rows contains molariform elements and only one lateral row on each side has enlarged teeth.

Coloration. The colours of live fishes are unknown.

Preserved material. Quiescent male. Ground colour dusky bronze, with a very faint mid-lateral stripe, six interrupted transverse bars and a distinct lachrymal stripe. Dorsal fin dark, lappets pale ; caudal dark except for its pale distal margin ; anal pale (? orange) with four, small, white ocelli arranged in a single row. Pelvics black on the outer two-thirds, lighter medially. *Females and immature males* uniformly light brown except for the darker dorsal head surface and nape ; a dark

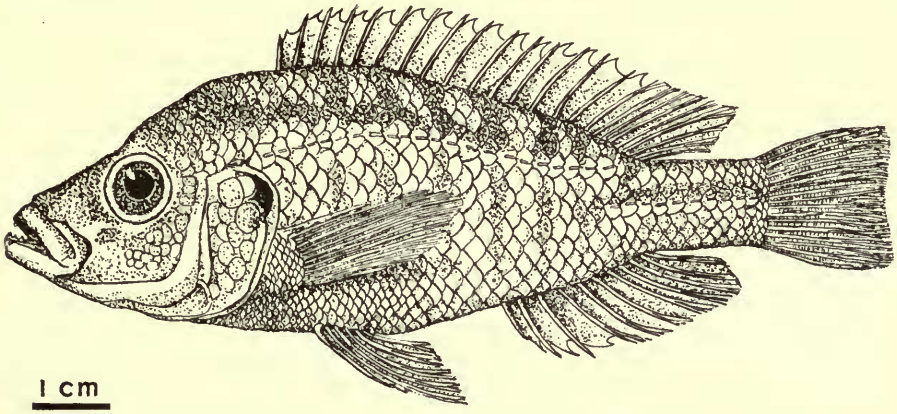

Fig. 15. *Haplochromis theliodon ;* holotype. Drawn by Miss G. Osterritter.

mid-lateral stripe of variable intensity is continuous in some specimens but interrupted in others above and slightly anterior to the anal fin ; when interrupted, the line is thickened to form a black blotch above the pectoral fin. A fainter, continuous dorsal stripe runs above the upper lateral line ; there are traces of seven to nine, variously interrupted transverse bars on the flanks but not on the caudal peduncle. Dorsal and anal fins hyaline, darker between the branched rays. Caudal maculate on the upper half, immaculate below. Pelvic fins hyaline in females but with the outer half dusky in males.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. The few specimens known came from two localities, both exposed, shallow and sandy beaches.

Food. Analysis of stomach and intestinal contents from all seven specimens indicate that *H. theliodon* is a bottom feeder with a varied diet including small fishes (cichlids, 20–25 mm. long), Gastropoda (foot and soft parts only), Lamellibranchiata and insect larvae, e.g. *Povilla adusta* (Ephemeroptera) and Trichoptera

(including the cases). Each fish had also ingested fairly large quantities of bottom debris.

Breeding. Few data are available; one female 75 mm. S.L. is sexually mature whilst another, 88 mm. S.L. appears to be a juvenile maturing for the first time.

Diagnosis and affinities. The nature of its lower pharyngeal bone and dentition places *H. theliodon* on the same level of structural modification as *H. humilior* and *H. riponianus*. In other characters (especially general appearance and oral dentition) *H. theliodon* is unlike both the former species. It differs from *H. humilior* in several morphometric characters (straight and not curved dorsal head profile, deeper preorbital, longer snout and smaller eye) and from *H. riponianus* in the shape of the head and the nature of its oral dentition. *Haplochromis theliodon* also differs from both the other species in having much smaller and more deeply embedded pectoral scales.

The affinities of *H. theliodon* are not easily determined except in so far as the species is clearly a little-modified derivative of the generalized stem. The small pectoral scales of *H. theliodon* are not common in generalized species still extant in Lake Victoria; but, small chest scales do characterize certain of the generalized and fluviatile species of East Africa, some of which also show an incipient hypertrophy of the pharyngeal bones and dentition (Greenwood, unpublished).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Tanganyika	
B.M. (N.H.).—1959.4.28.163 (Holotype)	Majita	E.A.F.R.O.
„ 1959.4.28.164–168	„	„
	Uganda	
„ 1959.4.28.169	Jinja Pier	„

Haplochromis empodisma sp. nov.
(Text-figs. 16 and 17)

Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 293; Regan, 1922, *Proc. zool. Soc. London*, 169.
Tilapia lacrimosa (part), Boulenger 1906, *op. cit.*, 450; *Idem*, 1915, *tom. cit.*, 234.
Haplochromis cinereus (part) Regan, 1922, *op. cit.*, 166.

Note. Because two specimens of *H. empodisma* (collected during Graham's 1927–28 survey of Lake Victoria) were mistaken for syntypes of *H. michaeli* Trewavas, this species was referred to as *H. michaeli* in previous papers (Greenwood, 1954, 1956*a*). All references to "*H. michaeli*" in these publications should now be corrected to read *Haplochromis empodisma.*

Holotype. An adult male 117 + 23 mm. total length (B.M. (N.H.) Reg. No.

1959.4.28.170), caught on the bottom in 90 feet of water off the southern tip of Kibibi Island (0° 10′ N.; 33° 10′ E.), Uganda.

Description, based on thirty-nine fishes (including the holotype) 65–117 mm. S.L.

Depth of body 33·0–43·8 (M = 39·3) per cent of standard length, length of head 33·3–39·4 (M = 36·7) per cent. Dorsal head profile straight or gently curved, sloping at an angle of 35°–40°. Preorbital depth 15·1–20·5 (M = 18·1) per cent of head; least interorbital width 20·6–28·6 (M = 24·3), length of snout 27·5–37·2 (M = 32·9), diameter of eye 24·4–34·0 (M = 27·3) per cent. Depth of cheek shows a marked positive allometry with standard length, being 21·2–23·0 per cent of head in fishes less than 80 mm. S.L. (N = 4) and 23·5–31·4 (M = 27·9) per cent in larger specimens (N = 35). Caudal peduncle 14·5–20·0 per cent of standard length and 1·3–1·7 (mode 1·4) times as long as deep.

Mouth horizontal or slightly oblique; lips not noticeably thickened. Posterior tip of the maxilla reaching the vertical through the anterior margin of the orbit or to

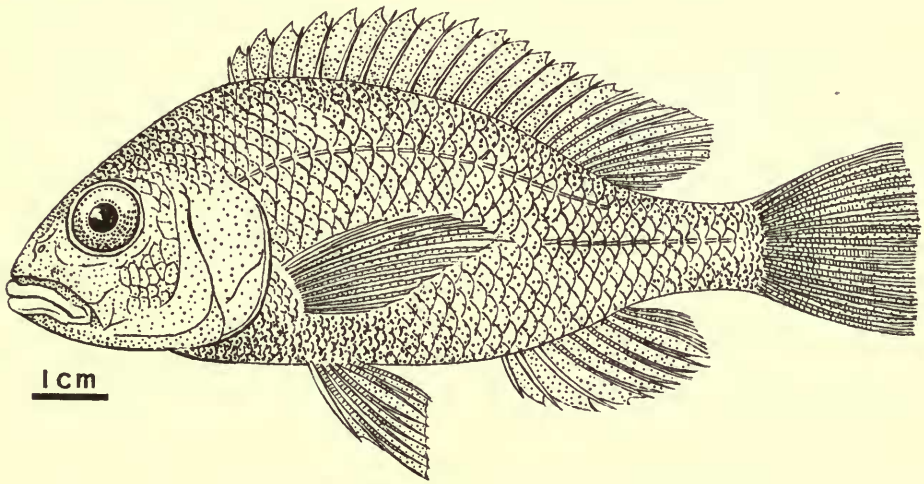

FIG. 16. *Haplochromis empodisma*; holotype. Drawn by John Norris Wood.

below the anterior part of the eye; less frequently, not reaching as far as the orbit. Lower jaw 39·1–48·7 (M = 43·9) per cent of head, 1·5–2·3 (mode, ill-defined, 2·0) times as long as broad. Malformation of the lower jaw is relatively common in this species; individuals so affected have the lower jaw broader than the upper (which closes within the lower) and are distinctly prognathous.

Gill rakers usually slender, although relatively stout rakers also occur; 7–10 (modal range 8–9) on the lower part of the first gill arch, the lowermost 1–3 rakers reduced, occasionally the uppermost 1 or 2 somewhat flattened and bi- or trifid.

Scales ctenoid; lateral line with 30 (f.10), 31 (f.9), 32 (f.15) or 33 (f.4) scales. Cheek with 3 or 4 (occasionally 5) series. Six or 7 scales between the lateral line and the dorsal fin origin, 6–8 between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.8), 24 (f.30) or 25 (f.1) rays, anal with 10 (f.1), 11 (f.22) or 12 (f.16), comprising XIV–XVI, 8 or 9 and III, 7–9 spinous and branched rays for

the fins respectively. Pectoral fin 73·0–96·5 (M = 85·8) per cent of head. Caudal truncate or sub-truncate.

Teeth. The teeth in the outer row of both jaws are slender and often gently recurved ; in fishes less than 95 mm. S.L. the teeth are unequally bicuspid but in larger individuals are weakly bicuspid or unicuspid ; it is usual to find both types of teeth in large fishes. There are 54–82 (modal range 70–72) teeth in the upper jaw.

Teeth forming the inner series are small and usually tricuspid but some unicuspids may occur, particularly in fishes over 100 mm. S.L. ; there are 2 or 3 (rarely 4) rows in the upper jaw and 1–3 in the lower. The innermost row, especially in the upper jaw, is implanted obliquely.

A common abnormality affecting both inner and outer teeth is for the crowns to be coarse, slightly swollen and darkly pigmented ; in such teeth the crown is globose.

Lower pharyngeal bone and teeth. The lower pharyngeal is fine and rather narrow,

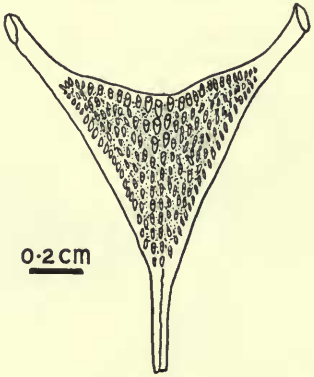

FIG. 17. *Haplochromis empodisma ;* lower pharyngeal bone, occlusal view.

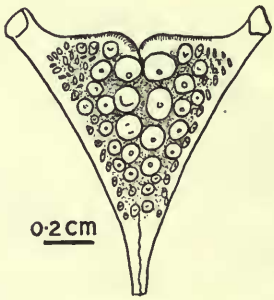

FIG. 18. *Haplochromis obtusidens ;* lower pharyngeal bone, occlusal view.

the dentigerous surface having the outline of an isosceles triangle. Usually, none of the pharyngeal teeth is markedly enlarged, but in certain specimens of all sizes a few teeth in the two median rows are slightly coarser. Even when enlarged these teeth retain the same form as their lateral and more slender congeners.

Osteology. The neurocranium and dentary of *H. empodisma* were figured and briefly described in an earlier paper (Greenwood, 1956*a*, p. 305, fig. 5 ; the species was then wrongly identified as *H. michaeli*). Both the neurocranium and the jaw elements are directly comparable with those of a generalized species such as *H. macrops*, except that in *H. empodisma* the outer teeth are more numerous.

Coloration in life. Sexually active males. Ground colour dark turquoise on the flanks and dorsal body surface, silver-yellow ventrally ; snout and dorsal head surface dark red. Dorsal and caudal fins diffuse red ; anal black anteriorly, dark red posteriorly, the ocelli orange-red. Pelvic fins black. *Quiescent males* as for females (see below) but dorsal fin with red maculae between the branched rays. Ripening males show some reddening of the head and snout, whilst the maculae of the dorsal

are more intense. *Females*. Ground colour yellowish-silver, darker dorsally. Dorsal and caudal fins dark neutral; anal yellow; pelvics very pale yellow.

Preserved material. *Males* (sexually active), dark grey becoming black ventrally; a distinct lachrymal stripe and two bars across the snout (quiescent males greyish brown, dusky on the belly; very faint indications of up to five incomplete transverse bars on the flanks; lachrymal stripe visible but no bars across the snout). Dorsal fin dark, the lappets black; caudal dark proximally, lighter distally; basal third of anal black, remainder of fin light, with two or three large white ocelli. Pelvic fins black. *Females* brownish-silver; in a few specimens there are very faint indications of a lachrymal stripe and of incomplete transverse bars on the flanks. All fins hyaline; in some fishes the upper half of the caudal is slightly maculate.

Distribution. Known only from Lake Victoria.

Ecology. *Habitat*. It seems that *H. empodisma* is generally restricted to those areas of the lake where the bottom is composed of organic mud. The species has been caught in bottom nets set at depths from 10–90 feet.

Food. The stomach and intestinal contents of thirty-seven fishes (from numerous localities) show that *H. empodisma* is a bottom feeder. The principal food organisms are the larval (and less frequently pupal) stages of dipterous insects, together with diatoms derived from the bottom mud. Only two fishes yielded remains of Mollusca; in one fish a few fragments of bivalve shell were found and in the other an operculum from a large gastropod. Since no other snail fragments were found in this fish, it is possible that the operculum was accidentally ingested.

Breeding. It is not known whether *H. empodisma* spawns in the habitats described above or whether spawning takes place over a more solid substrate, for example outcrops of rock or sand. Females carrying embryos and larvae have been caught together with non-breeding fishes. The smallest sexually active fish is a female 84 mm. S.L.; the smallest adult male is 90 mm. S.L. Both sexes reach the same maximum adult size.

Affinities. Structurally and in its feeding habits, *H. empodisma* must be considered a generalized species. It differs from the majority of generalized forms in Lake Victoria only by its larger size, greater number of teeth (possibly a correlate of the larger size) and in the wide range of depths at which it has been caught. The nearest living relative of *H. empodisma* is a small and as yet undescribed species which occurs in the same habitat but is confined to shallow water.

Haplochromis empodisma and *H. obtusidens* are strikingly similar except for one structure, the lower pharyngeal bone. In *H. obtusidens* the lower pharyngeal is thickened and carries a number of enlarged, crushing teeth, whereas in *H. empodisma* this bone is slender and carries numerous fine teeth. *Haplochromis empodisma* could well represent the ancestral type from which *H. obtusidens* was derived by an increase in size of the pharyngeal bones and a correlated change in the pharyngeal dentition. Although the inter-specific differences in the nature of the pharyngeal mill are fairly clear-cut, some individuals deviate from the specific mode in such a way as to indicate a likely transitional condition in the evolution of an "*obtusidens*"-like species.

Since, in turn, *H. obtusidens* provides a structural type basic to the evolution of a specialized crushing pharyngeal mill (as found in *H. ishmaeli* and *H. pharyngomylus*), *H. empodisma* could represent the extant representative of the basal species in the phyletic line which culminated in *H. ishmaeli* and *H. pharyngomylus*.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1959.4.28.170 (Holotype)	Off Kibibi Island	E.A.F.R.O.
,, 1906.5.30.472	Entebbe	Degen
,, 1906.5.30.402 (Paratype, *H. ishmaeli*)	Bunjako	,,
,, 1906.5.30.404 (Paratype, *H. ishmaeli*)	,,	,,
,, 1959.4.28.180–189	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.194–195	Thruston Bay	,,
,, 1959.4.28.196–197	Ekunu Bay	,,
,, 1959.4.28.198	Jinja	,,
,, 1959.4.28.199	Napoleon Gulf, near Jinja	,,
,, 1959.4.28.202–203	Kibibi Island	,,
,, 1959.4.28.358	Off S. tip of Kibibi Island	,,
	Tanganyika	
,, 1959.4.28.190–193	Nyamakyamwa	E.A.F.R.O.
	Kenya	
,, 1959.4.28.200–201	Manadu Island	,,
,, 1959.4.28.171–179	Off Port Southby	,,
	Lake Victoria, Locality Unknown	
,, 1928.6.2.37–38	—	M. Graham

Haplochromis obtusidens Trewavas 1928
(Text-fig. 18)

Haplochromis desfontainesi (part), Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 302.
Tilapia lacrimosa (part), Boulenger, 1915, *tom. cit.*, 234.
Haplochromis cinereus, (part) Regan, 1922, *Proc. zool. Soc. London*, 166.
Haplochromis obtusidens Trewavas, 1928, *Ann. Mag. nat. Hist.* (10), **2**, 95.

Lectotype. An adult male 107·0 + 23·0 mm. total length (B.M. (N.H.) Reg. No. 1928.5.30.21).

Description, based on forty-four specimens (including the lectotype and one paratype) 60–114 mm. S.L.

Certain proportions show fairly well-marked allometry with standard length ; for these, ranges and means are given for each of the relevant size-groups.

Depth of body 35·0–44·3 (M = 38·6) per cent of standard length, length of head 32·5–38·2 (M = 35·8) per cent. Dorsal head profile gently curved or, less commonly, straight, sloping at an angle of 40°–50°. Preorbital depth in fishes < 70 mm. S.L.

(N = 4), 13·0–16·7 (M = 14·5) per cent of head, in larger fishes (N = 40) 15·1–20·5 (M = 17·9); least interorbital width 21·8–29·0 (M = 24·2) per cent; snout length in fishes < 85 mm. S.L. (N = 6), 26·0–31·0 (M = 28·5) per cent, in larger individuals (N = 38), 29·0–36·4 (M = 33·3); diameter of eye in fishes < 85 mm., 27·6–34·8 (M = 31·2) per cent and in larger fishes 24·3–30·8 (M = 27·2); depth of cheek in specimens < 85 mm., 18·6–23·8 (M = 21·5) and in larger individuals 21·2–30·0 (M = 26·7) per cent of head. Caudal peduncle 15·2–19·7 (M = 17·5) per cent of standard length, 1·2–1·8 (mode 1·5) times as long as deep.

Jaws equal anteriorly; mouth horizontal or slightly oblique; lips not markedly thickened. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or to below the anterior part of the eye; exceptionally, not reaching the orbit. Lower jaw 37·9–45·5 (M = 41·8) per cent of head and 1·3–2·0 (mode 1·6) times as long as broad.

Gill rakers relatively slender, although short and stout rakers are found in a few individuals; 7–9 (modal range 7–8), rarely 6, on the lower part of the first arch, the upper pair of rakers often flattened.

Scales ctenoid; 29 (f.1), 30 (f.7), 31 (f.21), 32 (f.11) or 33 (f.4) in the lateral line; cheek with 3 or 4 (rarely 5) series; 5½–7 scales between the lateral line and the dorsal fin origin, 5–7 (rarely 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.13), 24 (f.25) or 25 (f.6) rays, anal with 11 (f.24), 12 (f.19) or 13 (f.1), comprising XIV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 73·5–103·0 (M = 86·8) per cent of head. Caudal truncate or sub-truncate.

Teeth. In fishes less than 90 mm. S.L., the outer row in both jaws is composed of unequally bicuspid and relatively slender teeth. Larger individuals have an admixture of either unequally bicuspid and unicuspid teeth or of weakly bi- and unicuspids. A few individuals have exclusively bicuspid or unicuspid teeth. There are 40–80 teeth (ill-defined mode at 70; modal range 66–70) in the outer row of the upper jaw.

Teeth in the inner series are generally tricuspid and small; in some fishes over 100 mm. S.L. there may be either a mixture of tri- and unicuspid teeth or, more rarely, only unicuspids. The innermost row of teeth (especially in the upper jaw) is implanted obliquely and in some individuals the whole inner series lie at an oblique angle. There are 2 or 3 (rarely 1 or 4) rows of inner teeth in the upper jaw and 1 to 3 (usually 2, rarely 4) in the lower.

Lower pharyngeal bone and teeth. Despite some individual variability, the lower pharyngeal bone of *H. obtusidens* is always obviously thickened and the two median rows of teeth are enlarged and molariform or sub-molariform. As might be expected, there is a positive correlation between size and the degree to which the pharyngeal bones and teeth are enlarged. In fishes over 90 mm. S.L. as many as six rows of teeth may be composed of molariform elements; even in specimens with a few molariform rows the remaining teeth are enlarged, except in the upper corners of the bone.

Osteology. In all respects except the form of the pharyngeal apophysis, the neurocranium of *H. obtusidens* resembles that of *H. empodisma*; the pharyngeal apophysis,

however, is stouter and broader, thereby foreshadowing the condition found in *H. ishmaeli* and *H. pharyngomylus*. In both these species the basioccipital facets are more expanded than in *H. obtusidens*.

Coloration in life. Sexually active males. Ground colour light blue-black with, ventrally, a silver patch extending from the isthmus almost to the vent ; branchiostegal membrane black. Dorsal fin dark with red lappets and margin to the soft part and red spots or dashes between the branched rays. Caudal dark with a blood-red margin and a diffuse red centre. Anal dark proximally, blood-red distally ; ocelli orange or orange-red. Pelvic fins black. *Quiescent males* as for females but lacking the red spots or flush on the dorsal fin. *Females.* Ground colour silver-grey. Dorsal fin dark with traces of a red flush. Caudal dark. Anal and pelvic fins yellowish.

Preserved material. Adult males. Ground colour brownish, dusky ventrally (below the level of the lower lateral line), with faint indications of four transverse stripes originating from the dark area but not reaching the base of the dorsal fin ; the intensity of the dusky area varies considerably, from charcoal to coal-black. Dorsal fin hyaline to dusky, the basal region and the lappets black ; soft part of the fin sometimes maculate. Caudal dark on its proximal half, light (yellowish) distally. Anal dark on the basal half to third, light distally, with two large white ocelli. Pelvic fins black. *Females* silver-grey to yellowish-brown ; in some fishes there are very faint indications of four to six, incomplete transverse bars on the flanks. Dorsal fin dark or hyaline. Caudal dark, the upper half maculate in some individuals. All other fins hyaline.

Note on four atypical individuals. Four specimens, 80–94 mm. S.L. (B.M. (N.H.) Reg. Nos. 1959.4.28.236–239) from Old Bukakata Bay, Uganda are included in the description given above although they differ from the generality of specimens in certain characters. The lower pharyngeal bones in two of these fishes are somewhat more slender than is modal but are typical in the other two specimens. All four fishes have fewer upper outer teeth than is usual (40–52 cf. modal range 66–70) and somewhat shallower cheek than equivalent sized specimens from other areas. In this latter character, however, they resemble the two type specimens. Finally it must be mentioned that these fishes resemble one another in general facies rather more closely than they resemble the other specimens. Such obvious but undefinable and geographically localized facies are fairly common amongst Lake Victoria *Haplochromis* species.

The exact status of the four specimens from Bukakata cannot be determined for want of more material from this locality.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. Haplochromis obtusidens is predominantly a species of shallow water (less than 30 feet), apparently restricted to a substrate of soft, organic mud ; a few individuals have, however, been taken over sand and in water about 60 feet deep.

Food. The gut contents of forty-six fishes (from numerous localities) indicate that the principal food organisms of *H. obtusidens* are insects (especially larval Diptera) and molluscs (particularly the bivalve *Corbicula*, although some gastropods

[*Melanoides*] are also eaten). Together with these organisms, the fishes had ingested fairly substantial quantities of bottom mud, which, in the areas inhabited by *H. obtusidens*, is almost entirely composed of living and moribund diatoms. A comparison of stomach and intestinal contents shows that the protoplasm of these diatoms is digested by the fish. Other plants, in this case mostly blue-green algae, are apparently undigested.

Breeding. *Haplochromis obtusidens* is a female mouth-brooder; exact spawning sites were not discovered. A male 83 mm. S.L. is the smallest mature fish in the sample studied; the smallest mature female is 89 mm. S.L. Both sexes reach the same maximum adult size.

Affinities. The relationships of *H. obtusidens* seem to lie with *H. empodisma* which it resembles in body-form and most syncranial characters. *Haplochromis obtusidens* differs in having an enlarged neurocranial apophysis for the upper pharyngeal bones and in the correlated character, enlarged pharyngeal bones and teeth. The species also shows certain fairly marked affinities with *H. ishmaeli* and *H. pharyngomylus* and could well represent the extant version of an ancestral type from which these two species evolved (see also p. 265).

In Lake Edward, *H. malacophagus* Poll has reached a comparable evolutionary stage leading towards extreme pharyngeal hypertrophy, but the two species are not closely related.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.531	Buganga	Degen
,, 1959.4.28.204–212	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.213–218	Ekunu Bay	,,
,, 1959.4.28.228–229	Pilkington Bay	,,
,, 1959.4.28.236–239	Old Bukakata Bay	,,
,, 1959.4.28.243–244	Dagusi Island	,,
,, 1959.4.28.245	Buka Bay	,,
,, 1959.4.28.247	Sesse Islands	,,
	Kenya	
,, 1909.7.27.43	Kavirondo Bay	Alluaud
,, 1959.4.28.219–227	Off Port Southby	E.A.F.R.O.
,, 1959.4.28.230–232	Kach Bay (Kavirondo Gulf)	,,
,, 1959.4.28.240–241	Beach below Usoma lighthouse	,,
,, 1959.4.28.242	Off Port Southby	,,
,, 1959.4.28.246	Kavirondo Gulf	,,
,, 1959.4.28.248	Off mouth of Nzoia River	,,
	Tanganyika	
,, 1959.4.28.233–235	Beach near Majita	,,
	Lake Victoria, Locality Unknown	
,, 1928.5.30.21 (Lectotype)	—	M. Graham
B.M. (N.H.).—1928.5.20.20 (Paratype)	—	,,

Haplochromis pharyngomylus Regan 1929
(Text-figs. 19 and 20)

Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446;
Idem, 1915, *Cat. Afr. Fish.*, 3, 293; Regan, 1922, *Proc. zool. Soc. London*, 169.
Haplochromis pharyngomylus Regan, 1929, *Ann. Mag. nat. Hist.* (10) **3**, 388.

Description, based on thirty-eight specimens (including the holotype) 70–126 mm. S.L.

Depth of body 33·8–42·0 (M = 38·5) per cent of standard length, length of head 31·5–36·8 (M = 34·6) per cent. Dorsal head profile straight or somewhat curved (occasionally concave between the eyes), sloping fairly steeply. Preorbital depth 13·8–19·0 (M = 16·8) per cent of head, least interorbital width 23·7–28·5 (M = 26·3), length of snout 27·3–33·3 (M = 30·8), diameter of eye 23·0–31·8 (M = 26·5), depth of cheek 19·7–27·0 (M = 24·1) per cent of head. Caudal peduncle 13·6–18·5 (M = 16·2) per cent of standard length, 1·1–1·6 (modal range 1·3–1·5) times as long as broad.

Mouth horizontal or slightly oblique, jaws equal anteriorly, the lower 35·8–44·0 (M = 38·6) per cent of head, 1·3–2·0 (mode 1·4) times as long as broad. Posterior tip of the maxilla reaching or almost reaching the vertical to the anterior orbital margin.

Gill rakers moderately stout, 6–8 (mode 7), rarely 9, on the lower part of the first arch, the lowermost 1 or 2 rakers reduced.

Scales ctenoid ; lateral line with 30 (f.1), 31 (f.6), 32 (f.12), 33 (f.13), 34 (f.4) or 35 (f.1) scales ; cheek with 3 or 4 series. Six or 7 (less frequently 8) scales between the lateral line and the dorsal fin, 7 or 8 (less frequently 6 or 9, rarely 10) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.7), 25 (f.28) or 26 (f.3) rays, anal with 11 (f.5), 12 (f.28) or 13 (f.5), comprising XV–XVI, 8–10 (rarely 11) and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 68·5–91·0 (M = 79·6) per cent of head. Caudal truncate.

Teeth. In fishes 70–90 mm. S.L. only unequally bicuspid, relatively stout teeth occur in the outer row of both jaws. Fishes 90–100 mm. S.L. show some variability in the form of these teeth, which may be unicuspids, a mixture of bi- and weakly bicuspid teeth or both bi- and unicuspids. There are 30–42 (mode 36, modal range 36–40) outer teeth in the upper jaw.

Teeth in the inner rows are usually tricuspid in fishes less than 100 mm. S.L. In larger individuals these teeth may be tricuspid or there can be a mixture of tri- and weakly tricuspids ; it is uncommon to find only unicuspid teeth in the inner rows. There are 2 or 3 (rarely 4) rows in the upper jaw and 1 or 2 (rarely 3) in the lower.

Lower pharyngeal bone and teeth. With one exception, the lower pharyngeal bone is massive, even in the smallest specimens. Nevertheless, a slight size correlated increase in relative stoutness can be detected in large fishes. Apart from *H. ishmaeli* (p. 277) and *Astatoreochromis alluaudi*, no other Lake Victoria Cichlidae have such large pharyngeal bones.

The exceptional specimen mentioned above was caught near Jinja and measured 98 mm. standard length. The lower pharyngeal of this fish can be compared with that of an *H. obtusidens* of a similar size. Since in all other respects this fish resembles *H. pharyngomylus* more closely than *H. obtusidens* it is included in the description of *H. pharyngomylus*. Four other specimens with even finer pharyngeal bones and dentition, but otherwise resembling *H. pharyngomylus*, are not included in the description but are dealt with in a separate appendix (p. 274).

The lower pharyngeal teeth of *H. pharyngomylus* are large and molariform except for a few teeth situated in the upper, lateral angles of the bone. These teeth, although relatively stout, are cuspidate and small; the number of such teeth decreases markedly in the largest individuals. By analogy with other species having

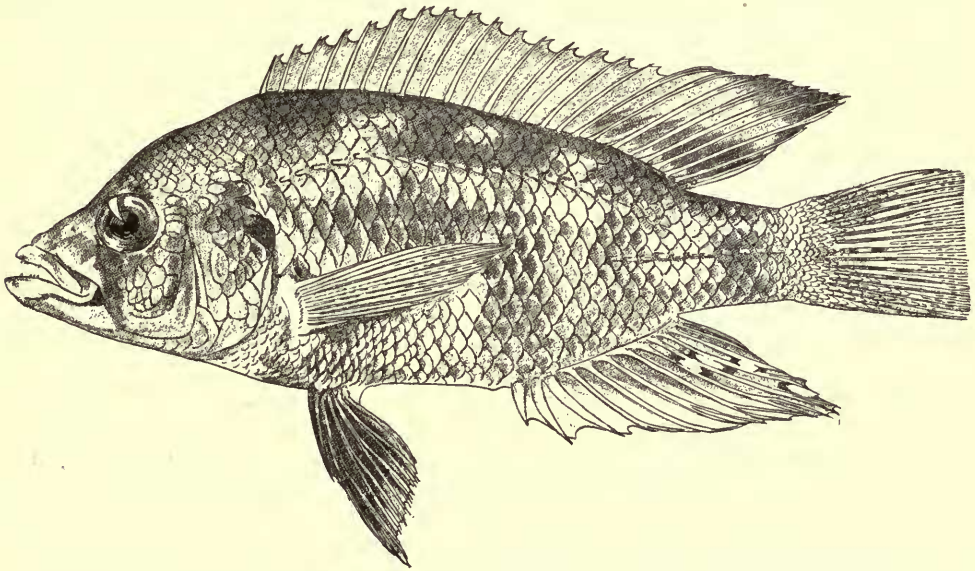

FIG. 19. *Haplochromis pharyngomylus*; holotype. Drawn by Miss M. Fasken.

enlarged pharyngeals and for which a greater size range of specimens is available is seems likely that small *H. pharyngomylus* should have less massive bones and fewer molariform teeth, confined to the median tooth series (see Greenwood, 1959).

Osteology of the neurocranium. Apart from an enlarged and strengthened articular apophysis for the upper pharyngeals, the neurocranium of *H. pharyngomylus* is that of a large, generalized *Haplochromis*. The apophysis has been figured and described previously (Greenwood, 1954). Compared with the apophysis of *H. obtusidens* that of *H. pharyngomylus* has a greater surface area and the prootic buttresses are more obvious. These characters are clearly correlated with the more massive pharyngeal bones and musculature of *H. pharyngomylus*. Only slight difrences exist in the apophyseal region of *H. pharyngomylus* and *H. ishmaeli*; but both species differ from *Astatoreochromis alluaudi* in the form taken by the various elements contributing to the apophysis (Greenwood, 1959. In that paper, I also

briefly described the possible effects and interactions of genetical and environmental factors on the development of apophyseal form and size in mollusc-crushing species).

Coloration in live fishes. Adult males. Ground colour blue-grey overlying silver; a distinct coppery sheen on the flanks. Dorsal fin hyaline with pinkish lappets and margin to the soft part. Anal hyaline, ocelli yellow. Caudal hyaline with a pink flush most intense distally and on the ventral half of the fin. Pelvics black. *Females.* Golden-green, becoming silvery-white ventrally. Dorsal and anal fins dark; the caudal yellowish-green, darker proximally.

Preserved material. Adult males. Greyish, darker in sexually active individuals; a dark lachrymal stripe sometimes visible; barring on the flanks variable, but usually consisting of seven to ten narrow vertical bars and a very faint longitudinal stripe following the course of the upper lateral line. Dorsal fin hyaline, dark basally in juvenile and quiescent fishes but almost black in sexually active individuals; lappets dark, the soft dorsal intensely maculate in sexually active fishes. Anal hyaline, dark basally, with five or six ocelli arranged in one or two horizontal rows.

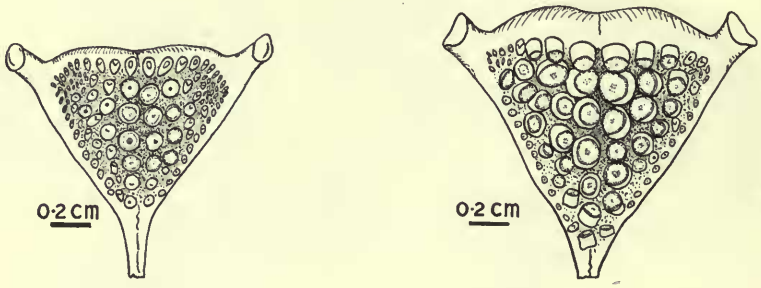

FIG. 20. *Haplochromis pharyngomylus;* lower pharyngeal bone, in occlusal view, of (*a*) a fish 98 mm. S.L., and (*b*) a fish 126 mm. S.L.

Caudal hyaline in quiescent fishes, dusky in active ones. Pelvics hyaline in juveniles, black in adults. *Females,* silvery-grey to light brown; striping variable; when present, as described for males. Dorsal fin hyaline or greyish, the soft part weakly maculate in adults. Caudal hyaline or dark, the upper half faintly maculate in some specimens. Anal and pelvic fins hyaline.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. Haplochromis pharyngomylus is apparently confined to water less than 40 feet deep and to areas of the lake where the bottom is hard (sand, shingle or, less frequently, rock); the species is often found amongst stands of aquatic plants. A few specimens have been caught in the areas of intergradation between sand and mud substrates.

Food. Analyses of stomach and intestinal contents from thirty specimens (representing most localities) show that fishes in the size-range 75–115 mm. S.L. feed mainly or even exclusively on Mollusca; only one fish had eaten mollusca and insect larvae. The sample examined also indicated that both bivalves and gastropods

are eaten in approximately equal proportions. The fragmented shells do not permit accurate identification of the prey species; *Sphaerium* sp. and *Corbicula* sp. were recognized amongst the bivalve remains and *Melanoides tuberculata* (the predominant snail), *Bellamya* and less frequently *Biomphalaria* amongst the gastropod fragments.

It is clear from the small size of most shell fragments that the pharyngeal mill in *H. pharyngomylus* is an efficient crushing mechanism. Yet, despite this powerful barrier some shells do pass into the stomach almost undamaged. Since these shells are invariably empty it seems that the digestive enzymes (especially those of the stomach) are capable of breaking down the bodies of snails without preliminary and physical assistance from the pharyngeal teeth. Trewavas (1938) noticed that the gut contents of *H. mahagiensis* (a mollusc eater from Lake Albert) were "impregnated and held in a hard mass by botryoidal aggregates of calcite. Whether these were formed before or after death and fixation is a matter for conjecture." My observations on the gut contents of *H. pharyngomylus* support Trewavas' observations only when the material had been fixed in formol. This would suggest that the calcite aggregates are formed as a result of a chemical reaction between the slightly acid formol and the calcium of the shell. I have never observed aggregates in fresh gut contents, where the various shell fragments could be separated easily.

Breeding. The actual spawning sites and breeding behaviour of *H. pharyngomylus* are unknown, but females carrying embryos and larvae in the buccal cavity occur together with non-breeding fishes in most localities. The smallest adult recorded is a female 90 mm. S.L.; the smallest adult male is 94 mm. S.L. Both sexes reach the same maximum adult size.

Affinities and diagnosis. Extreme hypertrophy of the pharyngeal mill serves to set *H. pharyngomylus* apart from all except one species of Lake Victoria *Haplochromis*. The other species is *H. ishmaeli* which appears to be very closely allied to *H. pharyngomylus*. Although in structural characters the two species are similar an experienced observer can, in most instances, readily distinguish between the two species. But, as is so often the case with *Haplochromis*, the subjective characters used for "field" identifications cannot be quantified or adequately described on paper. When seen alive, adult males of the two species have distinctive coloration.

Haplochromis pharyngomylus is distinguished from *H. ishmaeli* by the following characters: fewer outer teeth in the upper jaw (30–42, modal range 36–40 cf. 38–66, modal range 44–52 in *H. ishmaeli*); shorter pectoral fin (68·0–91·0, M = 79·6 per cent of head cf. 75·0–102·0, M = 88·5); differences in male breeding coloration (see p. 272 and p. 277) and differences in habitat preference (*H. pharyngomylus* is essentially a species of hard substrates whilst *H. ishmaeli* shows a marked preference for muddy areas). With the exception of differences in male breeding colours, none of these characters alone is trenchant; taken together, however, they provide fairly reliable diagnostic features.

The phylogenetic position of *H. pharyngomylus* has been discussed above (p. 269) and in an earlier paper (Greenwood, 1954).

In Lake Edward, *H. placodus* Poll represents the equivalent evolutionary phase in

the development of hypertrophied pharyngeals. *Haplochromis placodus* and *H. pharyngomylus* could be derived from a common ancestral stem, but of course, the two species could equally well be examples of convergent evolution.

APPENDIX

Four specimens (115–120 mm. S.L.) from Jinja (B.M. (N.H.) Reg. No. 1959. 4.28.352–355) bear a strong resemblance to *H. pharyngomylus* except that the lower pharyngeal bone in these specimens is barely enlarged and the pharyngeal dentition is correspondingly weak. These fishes cannot be distinguished from *H. pharyngomylus* on proportional measurements, teeth of jaws, fin and scale counts, general appearance or preserved coloration. All four fishes are adult males but unfortunately their live coloration was not recorded.

From *H. pharyngomylus* material described above and from field observations on numerous other specimens it is clear that intraspecific variability in the enlargement of the pharyngeal bones is slight and mainly correlated with size. No specimens were found which could be considered intermediate between the typical condition for the species and that seen in the aberrant individuals. On the other hand, a study of *Astatoreochromis alluaudi* (a *Haplochromis*-like monotypic genus) showed that some populations have enlarged pharyngeals whilst others exhibit only slight hypertrophy of these bones (Greenwood, 1959).

Thus for the moment it is impossible to dismiss the possibility that the four "*pharyngomylus*"-like fishes are indeed aberrant members of that species. I do not propose, however, to include them in this revised description or to describe them as distinct species until further collections dictate one step or the other.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.383	Entebbe	Degen
,, 1907.5.7.71	Buddu Coast	Simon
,, 1958.12.5.30–33	Entebbe	Pitman
,, 1959.4.28.317–321	Beach near Nasu Point	E.A.F.R.O.
,, 1959.4.28.322–326	Entebbe, Harbour	,,
,, 1959.4.28.327–329	Entebbe, Airport beach	,,
,, 1959.4.28.333–334	Beach near Grant Bay	,,
,, 1959.4.28.335–336	Between Yempita and Busiri Isls., Buvuma Channel	E.A.F.R.O.
,, 1959.4.28.340–343	Beach near Hannington Bay	,,
,, 1959.4.28.344	Entebbe, Harbour	,,
,, 1959.4.28.345–347	Napoleon Gulf, near Jinja	,,
,, 1959.4.28.351	Ramafuta Island	,,
,, 1959.4.28.358	Jinja Pier	,,
	Kenya	
,, 1959.4.28.348	Kasingiri Gingo (Kavirondo Gulf)	,,

Study material and distribution records (cont.)

Museum and Reg. No.	Locality	Collector
	Tanganyika	
,, 1959.4.28.337–339	Majita	,,
,, 1959.4.28.349	Beach near Majita	,,
,, 1959.4.28.350	Mwanza, Capri Bay	,,
	Lake Victoria, Locality Unknown	
,, 1928.5.24.313 (Holotype)	—	M. Graham
,, 1959.4.28.330–332	—	E.A.F.R.O.

Haplochromis ishmaeli Blgr. 1906
(Text-fig. 21)

Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 293; Regan, 1922, *Proc. zool. Soc. London*, 169.
Tilapia pallida (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 74; *Idem*, 1915, *tom. cit.*, 231–2.
Labrochromis pallidus Regan, 1920, *Ann. Mag. nat. Hist.* (9), **5**, 45 (footnote).
Tilapia martini (Part) Boulenger, 1915, *tom. cit.*, 239.
Paratilapia victoriana (part) Boulenger, 1915, *tom. cit.*, 341.
Haplochromis macrops (part) Regan, 1922, *Proc. zool. Soc. London*, 166.

In the original description of *H. ishmaeli*, Boulenger listed thirteen type specimens (syntypes) all collected by Degen at Bunjako, Uganda. However, only eleven specimens (ten in spirit and one skeleton) answering this description can be found in the collections of the B.M. (N.H.); furthermore, only eleven such specimens are recorded in the Museum's catalogue of accessions. That the number thirteen was a slip of the pen seems certain because Boulenger (1915) only lists ten types from Bunjako in the third volume of his Catalogue of Fresh-water Fishes of Africa. The only other specimen from this locality is listed in the "Catalogue" as a skeleton and is presumably the eleventh syntype.

These figures agree with the number of specimens I could locate and, more important, they agree with the number registered in the Museum's record of accessions. But, the situation is still somewhat obscure because in the "Catalogue" (*tom. cit. loc. cit.*) Boulenger lists as a type a specimen collected from *Entebbe*; since no reference is made to this fish in the original description I am treating its later inclusion in the list of types as erroneous.

Note on the genus Labrochromis, Regan, 1920. This genus, briefly described in a footnote to Regan's paper on the genera of Tanganyika cichlids was apparently based on a single specimen prepared from one of the syntypes of *T. pallida* (B.M. (N.H.) Reg. No. 1911.3.3.132). In his revision of the Lake Victoria Cichlidae, Regan (1922) correctly identified this skeleton as being that of *Haplochromis ishmaeli* and abandoned the genus *Labrochromis* on the grounds that, apart from possessing hypertrophied pharyngeals, *H. ishmaeli* is "nearly identical with *H. cinereus*." Whilst I do not agree with the latter part of this statement, I fully endorse Regan's action in not maintaining the monotypic genus *Labrochromis* for *Haplochromis ishmaeli*.

Lectotype of Haplochromis ishmaeli. An adult female 104·0 + 23·0 mm. total length (B.M. (N.H.) Reg. No. 1906.5.30.400) collected by Degen at Bunjako, Uganda.

Description, based on thirty-five specimens (including the lectotype and two paratypes) 82–136 mm. S.L., all from Lake Victoria. Two specimens from Lake Edward are described separately on p. 278.

Depth of body 37·0–45·5 (M = 40·1) per cent of standard length, length of head 33·8–37·5 (M = 34·8) per cent. Dorsal head profile slightly curved or straight, sloping fairly steeply. Preorbital depth 15·3–20·5 (M = 17·0) per cent of head, least interorbital width 24·0–32·0 (M = 27·6), length of snout 29·0–36·0 (M = 31·6), diameter of eye 23·0–31·0 (M = 27·7), depth of cheek 20·7–31·0 (M = 25·5) per cent. Caudal peduncle 14·6–18·8 (M = 17·6) per cent of standard length, 1·2–1·6

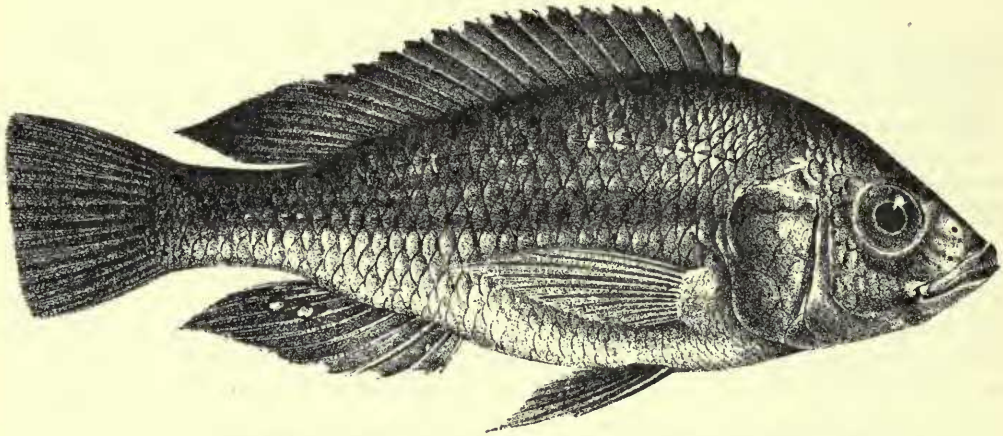

FIG. 21. *Haplochromis ishmaeli :* lectotype (from Boulenger, *Fishes of the Nile*).

(modal range 1·3–1·5) times as long as deep. Jaws equal anteriorly, the lower 35·8–42·5 (M = 39·1) per cent of head and 1·4–2·0 (modal range 1·4–1·6) times as long as broad. Mouth horizontal or very slightly oblique ; the posterior tip of the maxilla reaching the vertical through the anterior orbital margin or somewhat beyond, rarely not quite reaching the orbit.

Gill rakers stout, but relatively slender in a few specimens ; 6–8 (mode 7), rarely 9, on the lower part of the first arch, the lowermost one or two rakers usually reduced.

Scales ctenoid ; lateral line with 30 (f.3), 31 (f.8), 32 (f.15), 33 (f.5) or 34 (f.4) scales ; cheek with 3 or 4 rows. Five to 7 (rarely 8) scales between the lateral line and the dorsal fin origin ; 8–9 (occasionally 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.13) or 25 (f.21) rays, anal with 11 (f.13), 12 (f.21) or 13 (f.1) comprising XV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral fin 75·0–102·0 (M = 88·5) per cent of head. Caudal truncate or subtruncate.

Teeth. The outer row in both jaws usually contains a mixture of relatively stout, unequally bicuspid and unicuspid teeth ; less frequently only unicuspids occur in

this row. There is apparently no size-correlated difference in the type or the number of teeth present. There are 38–66 (modal range 44–52) teeth in the outer row of the upper jaw.

Teeth in the inner series are generally tricuspid, but in some fishes the entire inner series are composed of unicuspids. There are 2 or 3 (rarely 1) rows of teeth in the upper jaw and 1 or 2 (less commonly 3) rows in the lower. The inner teeth are implanted somewhat obliquely.

Lower pharyngeal bone and teeth. The lower pharyngeal bone in *H. ishmaeli* is massive and almost all the teeth are molariform ; only those situated in the posterior angles of the bone remain small, with pointed crowns. There is some individual variation in the relative enlargement of the bone, but this is slight in comparison with the variation known from such species as *H. obtusidens* and *Astatoreochromis alluaudi*. A slight size-correlated increase in the relative stoutness of the pharyngeal bones was observed in the material studied ; likewise, there is an increase in the number of molariform teeth in larger fishes.

In size, shape and dentition, the pharyngeal bones of *H. ishmaeli* are directly comparable with those of *H. pharyngomylus*.

Neurocranial osteology. The neurocranium of *H. ishmaeli* is virtually identical with that of *H. pharyngomylus*.

Coloration of live fishes. Sexually active males. Ground colour light yellow-green dorsally, shading to yellow on the flanks and greyish-white ventrally. Dorsal fin yellow-green, lappets of the anterior spines dusky, the remainder scarlet, as are the spots and dashes between the branched rays. Caudal fin greyish, with red maculae (sometimes coalesced) between the rays. Anal smoky grey with black lappets and an overall scarlet flush ; ocelli yellow. Pelvic fins black. *Females* golden-green shading to silvery-white ventrally, the pectoral region faintly blackish. Dorsal fin hyaline, with a narrow red margin. Anal light yellowish-green. Caudal and pelvic fins pale yellow.

Preserved material. Adult males, yellowish-grey, dusky on the chest and branchiostegal membrane (lighter in sexually quiescent fishes) ; very faint indications of six or seven vertical stripes on the flanks. (These bars are more widely spaced than in *H. pharyngomylus*, see p. 272). A distinct lachrymal stripe. Dorsal fin hyaline in juvenile fishes but darker and with the soft part maculate in mature males ; lappets dark. Caudal hyaline, the upper part often maculate. Anal hyaline, the basal third dark in sexually active individuals ; three to five large, dead-white ocelli arranged in one or, rarely, two rows. *Females*, brownish to yellowish-silver ; sometimes, very faint traces of five to seven transverse bars on the flanks ; a weak lachrymal stripe visible in some fishes. All fins hyaline, the dorsal darkest.

Distribution. Lakes Victoria and Edward.

Ecology. The data given in this section relate to fishes from Lake Victoria ; nothing is known for fishes from Lake Edward.

Habitat. Haplochromis ishmaeli is essentially a species of inshore regions where the water is less than 30 feet deep and the bottom composed of soft, organic mud.

No specimens have been recorded from depths greater than 60 feet, but some have been caught in nets set over sand and shingle substrates. *Haplochromis ishmaeli* would seem to be the ecological (soft substrate) counterpart of *H. pharyngomylus* (solid substrates).

Because of the difficulty in distinguishing *H. ishmaeli* from *H. pharyngomylus* and especially because the latter species was not recognized until after Graham's collections were brought to England, it is impossible to use Graham's (1929) catch records as an additional source of information on the intralacustrine distribution of *H. ishmaeli*.

Food. The stomach and intestinal contents of nineteen fishes (from several localities) indicate that *H. ishmaeli* in the size-range 84–135 mm. S.L. feed almost exclusively on Mollusca ; the few insect larvae found together with snails in the stomach of one fish suggest that insects may be ingested accidentally.

The number of fishes with food remains is insufficient to determine whether bivalves or gastropods predominate in the diet. Slightly more gastropods (*Melanoides tuberculata*) than bivalves (*Corbicula* sp.) were found in the sample examined.

Breeding. No information is available on the breeding sites or habits of *H. ishmaeli* although the number of females with " spent " ovaries and ventrally distended mouths suggests that the species is probably a female mouth-brooder. The smallest mature females are 97 mm. S.L. (but see Appendix 2) and the smallest adult male is 98 mm. S.L. Females apparently reach a greater maximum size than do males.

Affinities and diagnosis of *H. ishmaeli* are discussed on page 273, with reference to its closest relative, *H. pharyngomylus*.

APPENDIX

(1) *Haplochromis ishmaeli* from Lake Edward. I have been able to examine only two specimens from Lake Edward, one an adult female 120·0 + 28·0 mm. long and the other an adult male 118·0 + 27·0 mm. long (see Trewavas, 1933). In general appearance, in most morphometric characters and in scale and fin ray counts the two fishes are indistinguishable from specimens of a similar size from Lake Victoria. The nature of the pharyngeal bones and dentition is also identical. Nevertheless, the Lake Edward fishes do differ slightly in three characters.

(i) The interorbital is somewhat narrower (24·1 and 25·0 per cent of head) than the mean interorbital width of Victoria fishes (27·6 per cent) although still within the range known from this population. (ii) The number of outer teeth in the upper jaw (40 and 42) is in the lower section of the range for Lake Victoria fishes. (iii) The caudal peduncle is stouter in the majority of Victoria specimens. Now that more specimens are available from Lake Victoria, Trewavas' (op. cit.) observation on the larger eye of the Edward specimens is no longer applicable.

None of the differences commented upon above is so marked as those characterizing the Lake Victoria and Lake Edward populations of *Astatoreochromis alluaudi* (Greenwood, 1959).

Nothing is known about the bionomics of *H. ishmaeli* in Lake Edward ; the two specimens studied were caught in a seine net fished from the eastern shore of the lake near Kisenyi.

(2) Three *H. ishmaeli*-like fishes from Lake Victoria. Three specimens (82, 96 and 100 mm. S.L. (B.M. (N.H.) Reg. Nos. 1959.4.28.304–306)) caught in a trawl off the mouth of the Nzoia river, Kenya, present something of a problem. In appearance and in all standard counts and measurements these fishes are typically *H. ishmaeli*. However, their collector, Mr. S. H. Deathe, recorded the live coloration of these fishes as bright pink. Because all three specimens are adult males, I consider that this striking departure from the usual male coloration of *H. ishmaeli* may be significant, especially since pink is not one of the basic colours in *H. ishmaeli* pigmentation. A further interesting difference is that the smallest specimen is sexually mature whereas the smallest adult *H. ishmaeli* recorded is 98 mm. S.L.

Unfortunately I have only these three specimens and I did not see them when alive. Thus, it is difficult for me to assess fully this seemingly outstanding difference in coloration.

No typical *H. ishmaeli* were reported in the same haul and I do not consider that there is enough evidence to decide whether these peculiar individuals represent an aberrant population of *H. ishmaeli* or a distinct species differing from *H. ishmaeli* in the coloration of its adult males.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.400 (Lectotype)	Bunjako	Degen
,, 1906.5.30.401–402*a* (Paratypes)	,,	,,
,, 1906.5.30.396 (Paratype)	,,	,,
,, 1911.3.3.131 (Paratype *Tilapia pallida*)	Jinja	Bayon
,, 1909.5.4.8–10	Sesse Isls.	,,
,, 1906.5.30.275–279	Bunjako	Degen
,, 1959.4.28.281–290	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.296–300	Ekunu Bay	,,
,, 1959.4.28.301–303	Pilkington Bay	,,
,, 1959.4.28.307–309	Buka Bay	,,
,, 1959.4.28.312–313	Entebbe, Harbour	,,
,, 1959.4.28.314	Macdonald Bay	,,
,, 1959.4.28.316	0° 4′ S., 33° 14′ E.	,,
	Kenya	
,, 1909.11.15.40	Kisumu	A. B. Percival
,, 1959.4.28.274–280	South of Port Southby	E.A.F.R.O.
,, 1959.4.28.356	Kavirondo Gulf	M. Graham
	Tanganyika	
,, 1959.4.28.291–295	Majita	E.A.F.R.O.
,, 1959.4.28.310–311	Beach near Majita	,,

SUMMARY

1. Eleven species are redescribed on the basis of new material.

2. In addition, three new species (*Haplochromis theliodon*; *H. empodisma* and *H. saxicola*) are described.

3. Several phyletic lines are represented amongst these fourteen species, which include *H. cinereus*, a species once thought to represent one of the basic types from which the present-day species-flock had evolved. Evidence now available suggests that, anatomically, *H. cinereus* is not sufficiently generalized to retain this distinction.

4. Notes are given on the feeding habits and bionomics of the species.

5. Three species (*H. obtusidens*, *H. pharyngomylus* and *H. ishmaeli*) are largely or entirely mollusc-eaters; three others (*H. humilior*, *H. theliodon* and *H. riponianus*) feed on both insects and molluscs; one, *H. martini*, is a piscivorous predator and seven others are insectivore/omnivores.

6. One species, *H. niloticus* (nom. nov. for *Tilapia bayoni* Blgr. 1911) is known only from the Victoria Nile, whilst *H. ishmaeli* occurs in both Lakes Victoria and Edward; *H. humilior* is found in Lake Victoria and the Victoria Nile.

7. The assumed distribution of *H. macrops* in both Lakes Victoria and Edward is discussed; no definite conclusion can be drawn from the material now available.

8. Two groups of specimens are dealt with in separate appendices because of their uncertain taxonomic position. One group is apparently allied to or even conspecific with *H. pharyngomylus* and the other with *H. ishmaeli*. No conclusion can be reached on the status of these aberrant fishes.

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